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Introduction and Overview to Aquatic Acidification Studies in the Sudbury, Ontario, Canada, Area

W. Keller

Ontario Ministry of the Environment, 199 Larch Street, Sudbury, Ont. P3E 5P9, Canada

(JB557)

The mining and smelting of copper–nickel ore in Sudbury, Ontario, Canada (~46.5°N, 81°W), began in the early 1880's. Over time, initially very crude smelting practices, such as open roasting of ore on fuelwood piles, were replaced by ever more efficient recovery methods, production increased greatly, and tall stacks were constructed to disperse waste gases, particularly sulphur dioxide (SO_2). Watson and Richardson (1972), OCTF (1982), and Winterhalder (1984) provide summaries of the history of metal recovery activities in the Sudbury area.

Sulphur dioxide emissions from the Sudbury area smelters of INCO Limited and Falconbridge Nickel Mines Limited peaked in the 1950's and 1960's (Fig. 1) when annual average SO_2 emissions often exceeded 5000 t/d. In the last two decades, very large decreases in SO_2 emissions have been achieved (Fig. 1) as a result of process changes, regulation by government, and pollution control measures implemented by industry. During the 1980's, average SO_2 emissions remained below 2000 t/d. Further large-scale reductions in SO_2 emissions are scheduled for implementation by 1994 (MOE 1987).

In Canada, the extensive acidification of surface waters due to the atmospheric deposition of S was first recognized in the Sudbury area. Early studies by Gorham and Gordon (1960, 1963) showed low pH in lake and pond waters near the Sudbury metal smelters, caused by acidic deposition. Later, more geographically extensive surveys (Beamish and Harvey 1972; Conroy et al. 1974, 1976; Dillon et al. 1979; Pitblado et al. 1980) revealed that water quality problems associated with atmospheric emissions from the Sudbury smelters were not a local phenomenon, but affected a very large area of northeastern Ontario.

Based on survey data from over 200 lakes within a 200-km radius of Sudbury, a large zone (5300 km^2, containing a lake surface area of 650 km^2) of acidic ($pH < 5.5$) lakes was identified in the mid-1970's (Conroy et al. 1978; Keller et al. 1980). More recently, it has been estimated that over 7000 lakes within an area of 17 000 km^2 have been acidified to $pH < 6.0$ by the Sudbury emissions (Neary et al. 1990). In addition to elevated acidity, many of the lakes within the zone affected by Sudbury showed high concentrations of metals such as Al and Mn, related to accelerated leaching from watersheds by acid deposition. In the lakes closest to the Sudbury smelting complex, concentrations of metals abundant in the smelter emissions, notably Cu and Ni, were also often very elevated (Keller et al. 1980; Pitblado et al. 1980). Resulting biological effects due to water quality impairment were apparent at various aquatic trophic levels (Beamish and Harvey 1972; Sprules 1975; Kwiatkowski and Roff 1976; Roff and Kwiatkowski 1977; Keller and Pitblado 1984; Yan and Miller 1984; MacIsaac et al. 1987; and many others).

Since the initial documentation of the chemical and biological effects of acidification/metal contamination on aquatic systems, the Sudbury region has been a focus for much ongoing research. Results from Sudbury area studies have been instrumental in expanding our understanding of the impact of atmospherically conveyed contaminants on surface waters and in elucidating the mechanisms involved in this highly controversial research area. With the recognition of the widespread significance of the long-range transport of air pollutants, findings from Sudbury area studies have gained increased international relevance.

To some, "Sudbury Lake" conjures visions of a highly acidic/metal contaminated system, with a watershed denuded of vegetation and soil. Such lakes do exist, close to the smelters, as a legacy of severe fumigations and harsh historical logging practices. However, in reality, this stereotype is in sharp contrast with the rich diversity of aquatic systems in the Sudbury area. The views of very different "Sudbury" lakes provided in Fig. 2 are only a few representative examples of a continuum that grades from extremes.

Based on observed lake effects, the area clearly influenced by Sudbury emissions extends to over 100 km from the Sudbury smelters, and our overall area of interest extends to >200 km. Within this study area, with its profusion of surface waters (~20 000 lakes within 100 km of Sudbury; Cox 1978), the impacts of S and trace metal deposition associated with the Sudbury smelters range from extreme to nondetectable. In fact, a key characteristic of the area is the large gradient of lake types related both to differing contaminant deposition regimes, reflecting distance from the smelters (Jeffries 1984), and to great natural variability in catchment characteristics.

Although our study area is all on the Precambrian Shield, substantial local variations in specific bedrock geology and surficial deposits occur, which can greatly influence lake chemistry (e.g. Conroy and Keller 1976; Semkin and Kramer 1976; Jeffries et al. 1984). Long-term mean annual precipitation across this area of Ontario ranges from ~700 to 1000 mm of which ~100 to 300 mm falls as snow, and long-term mean annual unit runoff is ~300 to 500 mm (Government of Ontario 1984). Given the climatic and edaphic variations within our overall study area, it is not surprising that there is also substantial variation in forest cover. Sudbury is located in the Great Lakes St. Lawrence Forest Region, a transitional forest zone grading from the coniferous boreal forest to the north to the deciduous forest to the south. Specific lake catchments may contain mixed forest or be dominated by either coniferous or deciduous forest stands. Wetlands are commonly a major component of catchments in this area, particularly to the north and west of Sudbury (Government of Ontario 1984).

It is the variety of catchment types, atmospheric deposition regimes, and resultant lake types that in large measure provides

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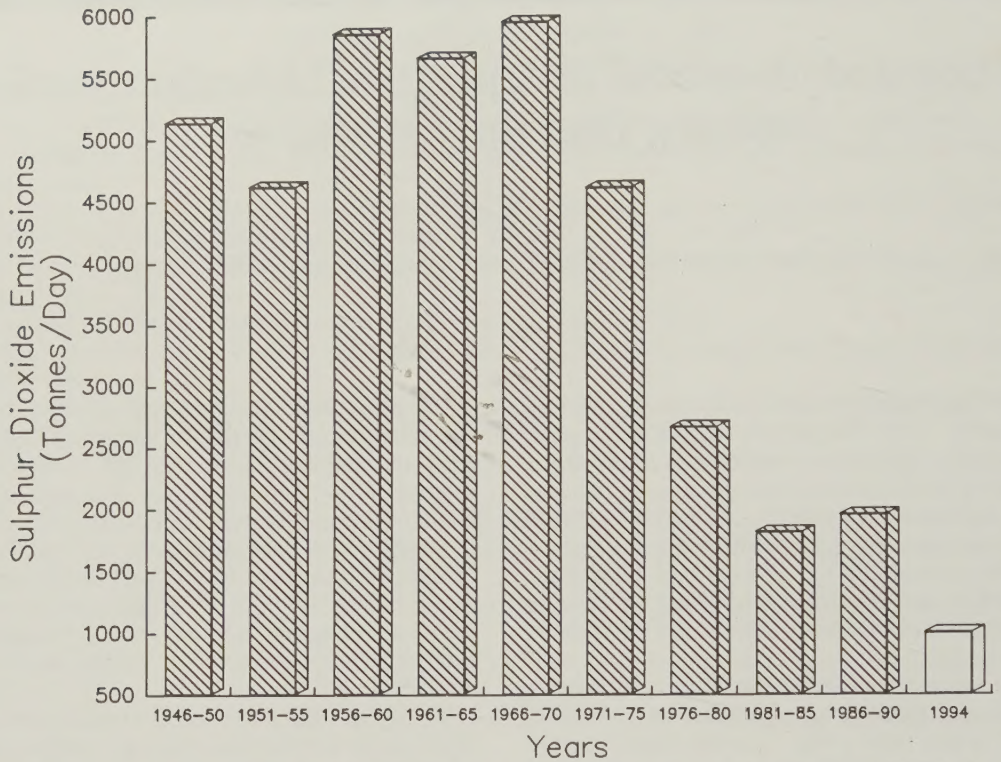

FIG. 1. Patterns in average daily SO_2 emissions in the Sudbury area for 5-yr intervals beginning in the mid-1940's. Emissions of SO_2 for INCO Limited and Falconbridge Nickel Mines Limited are combined. Projected emissions for 1994 (MOE 1987) are indicated by the open bar.

the great research possibilities in the Sudbury area; its attraction and suitability for diverse aquatic research activities are apparent from the references given in this paper, which constitute just a small sample of the studies conducted over the years. A recent compilation of aquatic, acidification-related publications involving the Sudbury area yielded over 200 citations (available from the author on request).

Work in the Sudbury area has, however, largely depended on the efforts of individuals, or specific institutions and agencies, without the benefit of overall coordination. In this collection of papers, we have attempted to bridge the gaps between disciplines, institutions, and agencies in order to assemble a diverse cross-section of work summarizing our current understanding of aquatic systems in the Sudbury area and the implications for lake acidification/metal contamination studies in general.

Many of the papers in this series draw on the variety of Sudbury area aquatic environments to examine the responses of various trophic levels across environmental gradients.

Conlon et al. (1992) examined fish community structure and lake trout (*Salvelinus namaycush*) presence in 30 low-alkalinity lake trout lakes spanning a wide range in pH and trace metal concentrations. Based on this analysis, they proposed a number of easily obtainable predictors (pH, alkalinity, conductivity) that should prove useful for large-scale monitoring of lake trout status in eastern North American lakes. Casselman and Gunn (1992) demonstrated that bony tissues in lake trout can also provide a useful population monitoring tool. Matuszek et al. (1992) used very extensive survey data to clearly place the damage to sportfish populations attributable to Sudbury smelter emissions in proper perspective. They demonstrated that in Ontario, almost all of the known acidification-related losses of lake trout, brook trout (*Salvelinus fontinalis*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Stizostedion vitreum*) have occurred in the Sudbury area.

Adverse effects on other aquatic trophic levels are also apparent in the Sudbury area. Glooschenko et al. (1992), based on examination of 118 potential amphibian breeding sites, demonstrated relationships between the occurrence of a number of amphibian species and breeding pond chemistry (acidity, trace metal concentrations). Similarly, acidification status was important in controlling the phytoplankton community structure of 111 Sudbury area lakes examined by Nicholls et al. (1992). Well-defined relationships were apparent between acidity and the number of phytoplankton taxa. McNicol and Wayland (1992) demonstrated that in 65 small Sudbury area lakes, acidity and fish species composition were important in distinguishing among different littoral macroinvertebrate assemblages, which in turn appeared to be a factor influencing habitat selection by some species of waterfowl.

Pitblado (1992) used extensive lake survey data from the Sudbury area to test the feasibility of using satellite-derived reflectance data for predicting water quality characteristics, particularly characteristics related to lake acidification. This technology holds considerable promise for future use as a water quality monitoring tool based on the relationships observed between reflectance and some key water quality parameters, notably dissolved organic carbon.

The great variability of lakes in the Sudbury region has also facilitated the selection of study sites for experimental manipulations. Keller et al. (1992b) documented the changes in zooplankton community structure that followed the neutralization (from pH 4.9 to >6.0) of acidic Bowland Lake with finely powdered limestone in 1983. While changes in the occurrence/abundance of some zooplankton species, consistent with apparent relationships to acidity, were observed in Bowland Lake

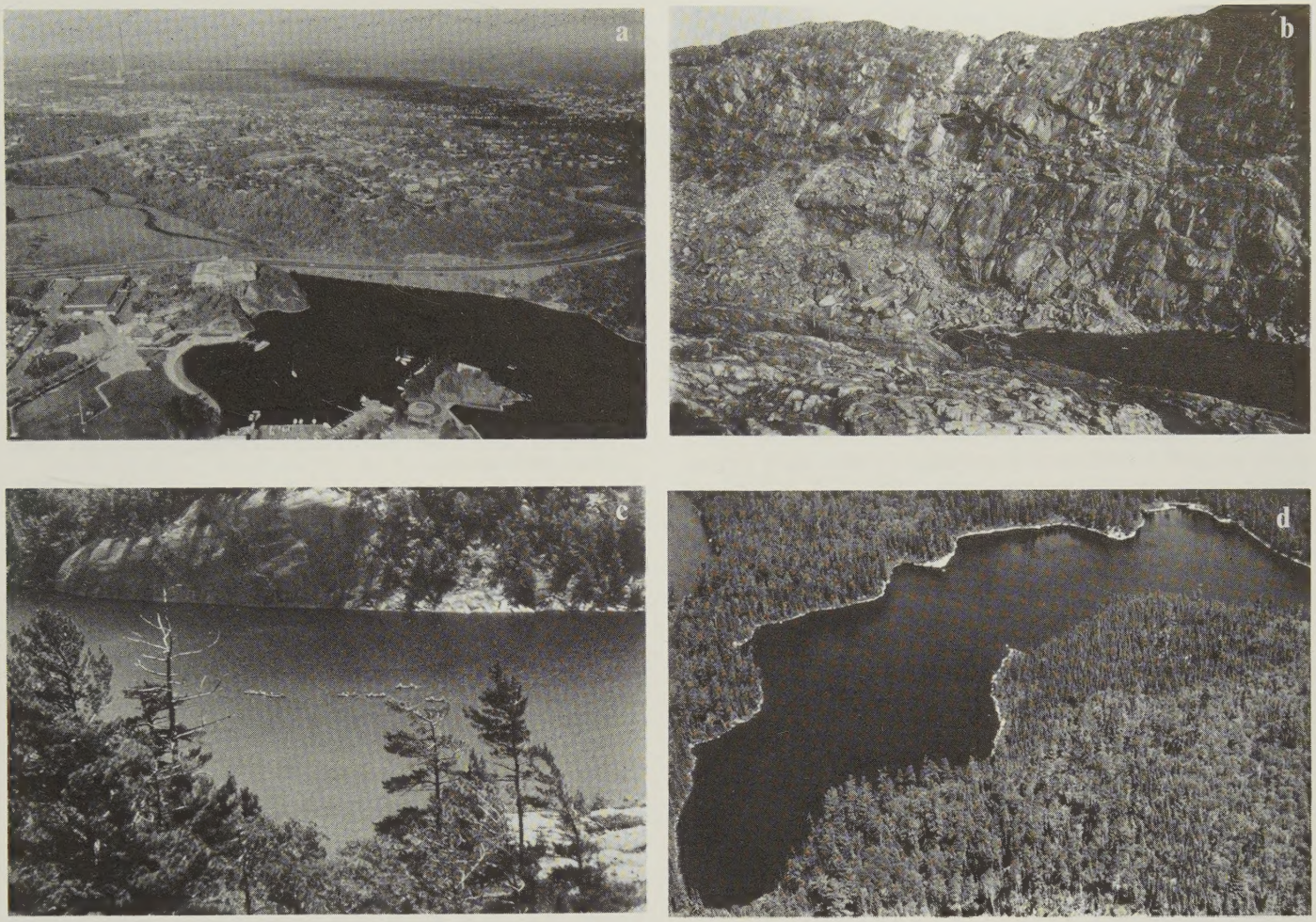

FIG. 2. Representative lakes within the Sudbury zone of effect. (a) Ramsey Lake, in the centre of the City of Sudbury. Because of inherently high buffering capacity, Ramsey Lake has never become acidified despite very high S loadings. (b) Daisy Lake, 8 km southeast of Sudbury, a highly acid, metal-contaminated lake. Portions of the Daisy Lake watershed were denuded of soils and vegetation through historical impacts of SO_2 fumigations, logging and fires. (c) George Lake, 56 km southwest of Sudbury. The focus of one of the first case studies documenting effects of acidification on fish in Ontario (Beamish et al. 1975), George Lake, like many other lakes in the Killarney Park Region, was very sensitive to acid inputs because of a highly weathering-resistant geological setting and sparse soil development. (d) Whirligig Lake, 106 km north of Sudbury. This is one of only two lakes that supported natural populations of aurora trout, a rare colour variant of the brook trout (*Salvelinus fontinalis*). Acidification resulted in the disappearance of these populations by the 1960's (Keller 1978).

after neutralization, overall patterns in the total abundance of zooplankton appeared to be related to other factors such as fish and *Chaoborus* predation and temperature fluctuations. Casselman and Gunn (1992) observed increased growth of lake trout otoliths in Nelson Lake after the lake was artificially neutralized from pH 5.7 to 6.4. Experiments involving acid additions to stream channels (Griffiths 1992) suggested that stream acidity is very important in organizing and maintaining lotic chironomid communities. Low pH (4.5) led to a community with few species and low abundance.

In addition to the great spatial variability in aquatic systems in the Sudbury area, substantial temporal changes in water quality associated with reduced smelter emissions were observed in the early 1980's (LaZerte and Dillon 1984; Hutchinson and Havas 1986; Keller and Pitblado 1986; Keller et al. 1986). These findings were of major significance because they provided the first conclusive proof that emission reductions do benefit aquatic systems in a reasonably short time frame — giving very powerful support to arguments for emissions abatement as a solution to the acid deposition problem.

Keller et al. (1992a) examined a relatively long-term (1981–89) data set for 42 Sudbury area lakes and demonstrated that while many Sudbury lakes remain highly acidic and metal contaminated, water quality improvements continued even under fairly static S emission levels, indicating the influence of lag time inherent in these systems. Almost a decade of monitoring on these lakes has also shown the importance of climatic fluctuations as an influence on temporal patterns in lake chemistry. A. S. Dixit et al. (1992) and S. S. Dixit et al. (1992) used modern paleolimnological techniques to examine truly long-term chemistry patterns. Using sediment cores from 71 Sudbury area lakes, S. S. Dixit et al. (1992) determined that lakes with current pH between 6.0 and 7.0 had either declined or increased in pH over the last century, while presently alkaline (pH $>$ 7.0) lakes had become more alkaline. Extensive acidification was apparent for most currently acidic (pH $<$6.0) lakes, and even the few naturally acidic lakes in the data set had acidified further during this century. Detailed chronological analysis of cores from three lakes (A. S. Dixit et al. 1992) showed some lake-specific variation in patterns of inferred pH;

however, in general, acidification appeared to commence in the 1920's or 1930's and became severe by the 1960's. Inferred pH increased during the last decade, offering further evidence for the chemical recovery of Sudbury lakes.

Documentation of chemical recovery has raised the even more compelling issue of biological recovery following emission reductions (Dixit et al. 1989; Gunn and Keller 1990; Keller and Yan 1991) because protection/restoration of aquatic communities is the ultimate goal of abatement efforts. Biological recovery is, of course, implicit in the documentation of chemical recovery by paleolimnological methods, as shown by A. S. Dixit et al. (1992). Clearly, chrysophyte and diatom assemblages respond quickly to reduced acidity. Through direct temporal analysis of phytoplankton community structure in seven Sudbury area lakes, Nicholls et al. (1992) also demonstrated that positive responses of phytoplankton communities, particularly increased numbers of phytoplankton taxa, have accompanied water quality improvements. Temporal patterns of recovery relative to changes in acidity in these lakes were essentially consistent with pH/phytoplankton relationships derived from spatial examination of lakes along an acidity gradient. Griffiths and Keller (1992) demonstrated that changes in the occurrence and abundance of benthic fauna have occurred in three Sudbury area lake basins and that these changes were consistent with a direct effect by the reduced acidity observed in the lakes. In these lakes, which are dominated by lake trout and yellow perch (*Perca flavescens*) populations, fish predation appeared to be a secondary factor influencing the composition and abundance of the zoobenthos community. In Nelson Lake, improved water quality, even before the lake was neutralized, apparently led to establishment of abundant hypolimnetic crustacean zooplankton populations that coincided with increased body and bony tissue growth in lake trout (Casselman and Gunn 1992).

Manipulation experiments in the Sudbury area have also provided valuable insights into the recovery process. Keller et al. (1992b) showed that significant changes in the species composition of planktonic rotifer and crustacean communities, toward assemblages more typical of near-neutral lakes, occurred in Bowland Lake after it was neutralized with $CaCO_3$. However, some acid-sensitive zooplankton species declined again, very early during the reacidification process when lake pH declined to <6.0. Griffiths (1992) showed that rapid reinvasion of acid-sensitive chironomids occurred in formerly acidified stream channels after acid additions were stopped. Within about 6 wk, chironomid communities resembled those in less acidic stream channels.

In summary, over two decades of aquatic studies in the Sudbury area have made and continue to make invaluable contributions to our knowledge of the effects of airborne contaminants on aquatic systems. While the Sudbury area continues to provide opportunites to quantify and understand the adverse effects of acid and metal deposition, it now has also become a unique field laboratory to examine the beneficial effects of emission reductions. Although many Sudbury area lakes are still highly acidic and metal contaminated, substantial chemical and biological improvements in aquatic systems have already occurred after reductions in emissions, which will continue to decline after 1994 (MOE 1987). In an encouraging turn of events, the area of Canada showing the most extreme impacts of atmospherically conveyed pollutants is now offering the opportunity to investigate, understand, and assist the recovery process in aquatic ecosystems damaged by atmospheric inputs of contaminants. It is hoped that this series of papers will provide a framework for future lake management strategies and continuing research in the Sudbury area and elsewhere.

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References

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Beamish, R. J., W. L. Lockhart, J. C. Van Loon, and H. H. Harvey. 1975. Longterm acidification of a lake and resulting effects on fishes. Ambio 4: 98–102.

Casselman, J. M., and J. M. Gunn. 1992. Dynamics in year-class strength, growth, and calcified-structure size of native lake trout (*Salvelinus namaycush*) exposed to moderate acidification and whole-lake neutralization. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 102–113.

Conlon, M., J. M. Gunn, and J. R. Morris. 1992. Prediction of lake trout (*Salvelinus namaycush*) presence in low-alkalinity lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 95–101.

Conroy, N. I., K. Hawley, and W. Keller. 1978. Extensive monitoring of lakes in the Sudbury area, 1974–1976. Ont. Minist. Environ. Tech. Rep. 40 p. plus appendices.

Conroy, N. I., K. Hawley, W. Keller, and C. Lafrance. 1976. Influences of the atmosphere on lakes in the Sudbury area. Proc. First. Spec. Symp. on Atmospheric Contribution to the Chemistry of Lake Waters. J. Int. Assoc. Great Lakes Res. 2: 146–165.

Conroy, N. I., D. S. Jeffries, and J. R. Kramer. 1974. Acid shield lakes in the Sudbury, Ontario region. Proc. Symp. Water Pollut. Res. Can. 9: 45–61.

Conroy, N. I., and W. Keller. 1976. Geological factors affecting biological activity in Precambrian Shield lakes. Can. Mineral. 14: 62–72.

Cox, E. T. 1978. Counts and measurements of Ontario lakes: watershed unit summaries based on maps of various scales by watershed unit. Ont. Minist. Nat. Resour. Rep., Toronto, Ont. 93 p. plus appendices.

Dillon, P. J., N. D. Yan, W. A. Scheider, and N. Conroy. 1979. Acidic lakes in Ontario: characterization, extent and responses to base and nutrient additions. Arch. Hydrobiol. Beih. 13: 317–336.

Dixit, A. S., S. S. Dixit, and J. P. Smol. 1992. Long-term trends in lake water pH and metal concentrations inferred from diatoms and chrysophytes in three lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 17–24.

Dixit, S. S., A. S. Dixit, and J. P. Smol. 1989. Lake acidification recovery can be monitored using chrysophycean microfossils. Can. J. Fish. Aquat. Sci. 46: 1309–1312.

1992. Assessment of changes in lake water chemistry in Sudbury area lakes since preindustrial times. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 8–16.

Glooschenko, V., W. F. Weller, P. G. R. Smith, R. Alvo, and J. H. G. Archbold. 1992. Amphibian distribution with respect to pond water chemistry near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 114–121.

Gorham, E., and A. G. Gordon. 1960. The influence of smelter fumes upon the chemical composition of lake waters near Sudbury, Ontario and upon the surrounding vegetation. Can. J. Bot. 30: 477–487.

1963. Some effects of smelter pollution upon aquatic vegetation near Sudbury, Ontario. Can. J. Bot. 41: 371–378.

Government of Ontario. 1984. Water quantity resources of Ontario. Ont. Gov. Interminist. Rep. 71 p.

Griffiths, R. W. 1992. Effects of pH on community dynamics of Chironomidae in a large river near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 76–86.

Griffiths, R. W., and W. Keller. 1992. Benthic macroinvertebrate changes in lakes near Sudbury, Ontario following a reduction in acid emissions. Can. J. Fish Aquat. Sci. 49 (Suppl 1): 63–75.

Gunn, J. M., and W. Keller. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

HUTCHINSON, T. C., AND M. HAVAS. 1986. Recovery of previously acidified lakes near Coniston, Canada following reductions in atmospheric sulphur and metal emissions. Water Air Soil Pollut. 29: 319–333.

JEFFRIES, D. S. 1984. Atmospheric deposition of pollutants in the Sudbury area, p. 118–154. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons, New York, NY.

JEFFRIES, D. S., W. A. SCHEIDER, AND W. R. SNYDER. 1984. Geochemical interactions of watersheds with precipitation in areas affected by smelter emissions near Sudbury, Ontario, p. 196–241. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons Inc., New York, NY.

KELLER, W. 1978. Limnological observations on the aurora trout lakes. Ont. Minist. Environ. Tech. Rep., Sudbury, Ont. 48 p.

KELLER, W., J. M. GUNN, AND N. I. CONROY. 1980. Acidification impacts on lakes in the Sudbury, Ontario, Canada area, p. 228–229. *In* D. Drablos and A. Tollan [ed.] Ecological impacts of acid precipitation. Proc. Int. Conf. Ecol. Impacts Acid Precip. Sandefjord, Norway.

KELLER, W., AND J. R. PITBLADO. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acidic deposition. Water Air Soil Pollut. 23: 271–291.

1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water Air Soil Pollut. 29: 285–296.

KELLER, W., J. R. PITBLADO, AND J. CARBONE. 1992a. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 25–32.

KELLER, W., J. R. PITBLADO, AND N. I. CONROY. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. Water Air Soil Pollut. 31: 765–774.

KELLER, W., AND N. D. YAN. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

KELLER, W., N. D. YAN, T. HOWELL, L. A. MOLOT, AND W. D. TAYLOR. 1992b. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 52–62.

KWIATKOWSKI, R. E., AND J. C. ROFF. 1976. Effects of acidity on the phytoplankton and primary productivity of selected northern Ontario lakes. Can. J. Bot. 54: 2546–2561.

LAZERTE, B. D., AND P. J. DILLON. 1984. Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario. Can. J. Fish. Aquat. Sci. 41: 1664–1677.

MACISAAC, H. J., T. C. HUTCHINSON, AND W. KELLER. 1987. Analysis of planktonic rotifer assemblages from Sudbury, Ontario area lakes of varying chemical composition. Can. J. Fish. Aquat. Sci. 44: 1692–1701.

MATUSZEK, J. E., D. L. WALES, AND J. M. GUNN. 1992. Estimated impacts of SO_2 emissions from Sudbury smelters on Ontario's sportfish populations. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 87–94.

MCNICOL, D. K., AND M. WAYLAND. 1992. Distribution of waterfowl broods in Sudbury area lakes in relation to fish, macroinvertebrates, and water chemistry. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 122–133.

MOE (ONTARIO MINISTRY OF THE ENVIRONMENT). 1987. Countdown Acid Rain, summary and analysis of the second progress reports by Ontario's four major sources of sulphur dioxide. Ont. Minist. Environ. Rep., Toronto, Ont. 17 p.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ont. Minist. Environ. Tech. Rep., Dorset, Ont. 146 p. plus appendices.

NICHOLLS, K. H., L. NAKAMOTO, AND W. KELLER. 1992. Phytoplankton of Sudbury area lakes (Ontario) and relationships with acidification status. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 40–51.

OCTF (ONTARIO/CANADA TASK FORCE). 1982. Report of the Ontario/Canada Task Force for the development and evaluation of air pollution abatement options for INCO Limited and Falconbridge Nickel Mines Limited in the Regional Municipality of Sudbury, Ontario. Intergovernmental Task Force Report, Toronto, Ont. 255 p.

PITBLADO, J. R. 1992. Landsat views of Sudbury (Canada) area acidic and nonacidic lakes. Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 33–39.

PITBLADO, J. R., W. KELLER, AND N. I. CONROY. 1980. A classification and description of some northeastern Ontario lakes influenced by acid precipitation. J. Great Lakes Res. 6: 247–257.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

SEMKIN, R. G., AND J. R. KRAMER. 1976. Sediment geochemistry of Sudbury-area lakes. Can. Mineral. 14: 73–90.

SPRULES, W. G. 1975. Midsummer crustacean zooplankton communities in acid stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

WATSON, W. Y., AND D. H. RICHARDSON. 1972. Appreciating the potential of a devastated land. For. Chron. 48: 312–315.

WINTERHALDER, K. 1984. Environmental degradation and rehabilitation in the Sudbury area. Laurentian Univ. Rev. 16: 15–47.

YAN, N. D., AND G. E. MILLER. 1984. Effects of deposition of acids and metals on chemistry and biology of lakes near Sudbury, Ontario, p. 244–282. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons, Inc., New York, NY.

Assessment of Changes in Lake Water Chemistry in Sudbury Area Lakes since Preindustrial Times

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Surface (recent) and bottom (pre-1880s) sediment samples from each of 72 Sudbury area lakes were analyzed for diatom valves and chrysophyte scales, and using these microfossils, we inferred changes in lake water pH, [Al], [Ni], conductance, and [Ca]. The study shows that extensive acidification has occurred in presently acidic (pH < 6.0) Sudbury lakes. Inferred [Al] has also increased in these lakes. The region also contains a few naturally acidic lakes; however, even these lakes have acidified further since the bottom sediments were deposited. Lakes that have current measured pH between 6.0 and 7.0 have either declined or increased in inferred pH in the past, whereas all lakes that are presently alkaline (pH > 7.0) have become more alkaline. The increase in inferred [Ni] in most of the study lakes indicates that Ni inputs are mainly atmospheric. Our data suggest that, in general, ion concentrations have increased in Sudbury lakes. The extent of acidification or alkalification in Sudbury lakes was primarily a function of proximity of the lakes to the smelters, orientation of prevailing wind patterns, and differences in watershed geology.

Nous avons analysé les échantillons des sédiments et de fond (avant 1880) prélevés dans chacun de 72 lacs de la région de Sudbury afin d'y trouver des valves de diatomées et des écailles de chrysophytes et, à l'aide de ces microfossiles, nous en avons déduit les changements qui se sont produits au niveau du pH, de la concentration d'Al, de la concentration de Ni, de la conductance et de la concentration de Ca dans les eaux des lacs. L'étude montre qu'une acidification prononcée s'est produite dans les lacs de Sudbury qui sont actuellement acides (pH $< 6,0$). La concentration d'Al déduite a également augmenté dans ces lacs. La région compte également quelques lacs qui sont naturellement acides; toutefois, même ces lacs se sont acidifiés encore depuis le dépôt des sédiments de fond. Dans le cas des lacs dont le pH actuel mesuré est compris entre 6,0 et 7,0, le pH déduit a soit décliné, soit augmenté par le passé, tandis que tous les lacs qui sont actuellement alcalins (pH $> 7,0$) sont devenus plus alcalins. L'augmentation de la concentration de Ni déduite dans la plupart des lacs de l'étude indique que les apports de Ni sont pour l'essentiel d'origine atmosphérique. Les données que nous avons obtenues semblent indiquer que les concentrations ioniques ont d'une manière générale augmenté dans les lacs de la région de Sudbury. Le degré d'acidification ou d'alcalinisation de ces lacs est principalement fonction de la distance séparant les lacs des fonderies, de la direction des vents dominants et des différences au niveau de la géologie des bassins hydrographiques.

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Metal mining began in the Sudbury region in 1883 when Ni ore was first discovered (Howard-White 1963). Open pit roasting started in 1888 at Copper Cliff, and mining and smelting activity greatly increased after the Coniston and Falconbridge smelters began operating in 1913 and 1920, respectively, and the 155-m-high stack was installed at Copper Cliff in the 1920s. Sulfur dioxide and trace metal emissions from the Sudbury smelters have been detrimental to lake water quality and aquatic biota located as far away as 100 km from the smelters (Beamish and Harvey 1972; Keller et al. 1986). Regional water chemistry surveys have indicated that there are many acidic lakes in and around Sudbury (e.g. Ontario Ministry of the Environment 1984) and that there has been biological damage to the ~7300 lakes which have pH < 6.0 in an area of 17 000 km^2 around Sudbury (Neary et al. 1990). However, within the last two decades, reductions in SO_2 and trace metal emissions by almost 50% have resulted in chemical and biological recovery of some Sudbury lakes (Dillon et al. 1986; Keller et al. 1986, 1992; Dixit et al. 1989a; Dixit et al. 1992a; Gunn and Keller 1990).

Because preindustrial water chemistry data are not available, indirect approaches must be used to infer long-term trends in water quality. Paleolimnological techniques, using sedimentary diatom and chrysophyte assemblages as biomonitors of limnological change, are now considered by many to be the most appropriate approach to reconstruct past limnological changes (Charles et al. 1989; Battarbee et al. 1990; Dixit et al. 1992) and to validate chemical models (Sullivan et al. 1990). Sedimentary diatom and chrysophyte assemblages have also been successfully used to detect trends in recent lake water recovery associated with the post-1970 reductions in SO_2 emissions (Dixit et al. 1989a; Dixit et al. 1992a, 1992b; Dickman and Rao 1989; Cumming 1991).

Although most research on algal microfossils has focused on reconstructing lake water pH, workers have recently begun inferring other environmental variables (Kingston and Birks 1990; Birks et al. 1990a; Dixit et al. 1991). For example, using surface sediment diatom assemblages from 72 Sudbury lakes, Dixit et al. (1991) developed inference models for lake water

pH, total [Al], [Ni], [Ca], and conductance and reconstructed these variables for a Sudbury lake.

A detailed assessment of postindustrial changes in lake water characteristics requires a continuous temporal record of algal microfossils. However, it is logistically prohibitive to analyze complete sediment cores from a large number of lakes, especially when the objective of the study is to provide regional estimates of overall limnological change. For such large-scale studies, the most effective approach is to restrict microfossil analysis to the top (recent) and bottom (preindustrial) sediment samples of lake cores (Charles and Smol 1990). The difference between preindustrial and recent inferences provides an estimate of the change in lake water chemistry as a result of anthropogenic activity and also provides information on "background" or "reference" limnological conditions. This approach has been succesfully used to provide regional estimates of lake water chemistry changes (e.g. pH, ANC, monomeric [Al], and dissolved organic carbon) in the Adirondack region of New York (Sullivan 1990; Sullivan et al. 1990; Cumming et al. 1992).

The objectives of our study are to use diatom and chrysophyte assemblages in the "tops" and "bottoms" of 72 lake sediment cores and to characterize preindustrial lake water chemical characteristics (pH, total [Al], [Ni], [Ca], and conductance), so as to examine the magnitude of changes in our study lakes since preindustrial (~1880s) times. Our chemical inferences are based on the predictive models developed from the surface sediment (top 0.25-cm section) diatom (Dixit et al. 1991) and chrysophyte (Dixit et al. 1989b) assemblages of these 72 calibration lakes. This study provides an overall assessment on how Sudbury area lakes have responded to metal mining and smelting activity.

Study Area and Study Lakes

Seventy-two lakes were selected for this study within a 100-km radius of Sudbury (Fig. 1), the limnological characteristics of which are described in Dixit et al. (1989b, 1991). The regional geology is characterized by Precambrian metamorphic, plutonic, and volcanic silicate Canadian Shield rocks, generally overlain by thin Pleistocene glacial deposits. Terrestrial vegetation grades from deciduous and coniferous forests in the south to coniferous forests in the north. The region contains a large number of acidic (pH $\leq$ 5.6), metal-contaminated, unproductive lakes, as well as some alkaline, nutrient-rich sites. Lakes were selected to reflect a large gradient of pH and metal concentrations, which are influenced by the lakes' bedrock geology, the prevailing wind patterns, and the lakes' proximities to acid and metal sources (see Fig. 1). Detailed paleolimnological studies have already been completed for some of these Sudbury lakes to study the timing, magnitude, and rate of acidification (Dixit et al. 1987, 1989a, 1989b, 1991; Dixit et al. 1992a, 1992b).

Materials and Methods

Short sediment cores (about 30 cm long) were obtained from 30 lakes in 1984 and 42 lakes in 1987, from or near the deepest points of our 72 lakes using a modified Kajak-Brinkhurst gravity corer equipped with a Plexiglas tube (internal diameter 6.5 cm). The cores were sectioned using a vertical extrusion device, similar to the one described by Glew (1988). The surface (top 0.25-cm section, representing recent conditions) and bottom sediment (usually from >20 cm depth, representing preindustrial conditions) samples from each of the 72 lakes were used in this study. The bottom sediment samples from all of the 30 lakes that we have ^{210}Pb dates for represent pre-1880s conditions. These 30 lakes are part of the 72 study lakes. These data suggest that most (if not all) of our bottom samples actually represent preindustrial conditions.

The sediment samples were acid cleaned (Dixit 1986), and quantitative slides were prepared using Battarbee (1973) trays. An attempt was made to count a minimum of 400 diatom valves and 400 chrysophyte scales; however, in 12 samples, chrysophyte scale counts remained low (e.g. <100) due to the paucity of scales. Because chrysophyte scales were not found in the bottom samples of eight lakes (Frederick, M2, Pigeon, McFarlane, Deer, Fairbank, Little Panache, and Lewis), we can only present chrysophyte-inferred pH changes for 64 lakes. Diatom-inferred changes are presented for 71 lakes because we could not retrieve bottom sediments from Frederick Lake (No. 11).

Weighted-averaging calibration and regression models, developed from the surface sediment diatom (Dixt et al. 1991) and chrysophyte (Dixit et al. 1989b) assemblages of the 72 Sudbury calibration lakes, were used to infer limnological changes from our microfossil assemblages. Diatom inferences were computed for pH, total [Al], [Ni], conductance, and [Ca]. Only pH inferences were computed using chrysophyte assemblages because, in the calibration data set, chrysophytes did not provide independent signals for other environmental variables. The diatom inference models use simple weighted-averaging with inverse deshrinking for pH, [Al], [Ni], conductance, and [Ca] (Dixit et al. 1991). The chrysophyte-inferred pH model is based on tolerance weighted-averaging with inverse deshrinking. The statistics for calibration models are presented in Table 1. For details on our predictive models, see Dixit et al. (1991). The use of weighted-averaging regression and calibration in paleolimnological research has been discussed by ter Braak and van Dam (1989), Birks et al. (1990a, 1990b), and Line and Birks (1990).

Results and Discussion

Floristic Changes

Algal assemblages have changed dramatically in many of our study lakes (Fig. 2 and 3). The recent diatom distributions (tops) indicate some definite trends when examined against the present-day measured lake water pH (Fig. 2). In low-pH lakes, indicators of acidic waters are common (e.g. acidobiontic and acidophilous *Eunotia* species, *Frustulia rhomboides* v. *saxonica*, *Asterionella ralfsii* v. *americana*, and *Melosira* (= *Aulacoseira*) *distans*) whereas in high-pH lakes, circumneutral and alkaline diatoms are common (e.g. *Melosira ambigua*, *Achnanthes minutissima*, *Anomoeoneis* (= *Brachysira*) *vitrea*, and *Asterionella formosa*). Many of the diatoms common in our acidic lakes also have high optima for metal concentrations (see discussion in Dixit et al. 1991). As we observed in the calibration study (Dixit et al. 1991), pH-indifferent diatoms (e.g. *Cyclotella stelligera* and *Tabellaria flocculosa* strain IIIp) showed no definite trend with respect to the pH gradient.

The common diatom taxa present in recent sediments were also found in the preindustrial sediments; however, in the bottom samples, their percent abundance did not indicate any distinct trends with respect to the present-day measured pH. Our floristic data indicate that, prior to industrial activity, the limnological characteristics of the study lakes were much more similar and homogeneous than they are today. Specifically, the

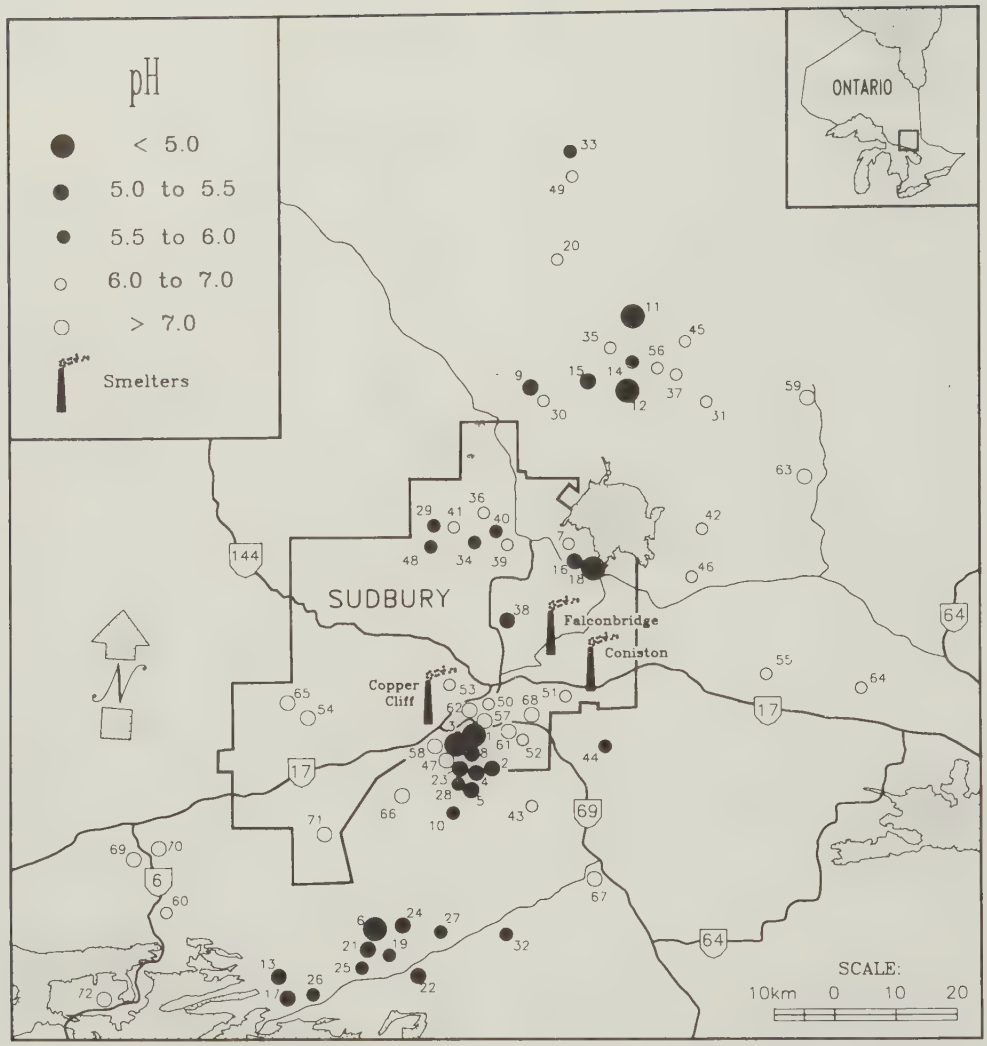

FIG. 1. Study area showing the location of the 72 study lakes. In order to show spatial patterns in present-day diatom-inferred pH in the study region, the lakes are marked by symbols representing five pH categories. 1, Silver; 2, Pine; 3, Crooked; 4, Clearwater; 5, Unnamed 2; 6, Ruth-Roy; 7, M4; 8, Lohi; 9, Mountaintop; 10, Wavy; 11, Frederick; 12, Chiniguchi; 13, Acid; 14, Unnamed 1; 15, Telfer; 16, M1; 17, Lumsden; 18, M2; 19, Johnnie; 20, Laundrie; 21, Terry; 22, Mahezenazing; 23, Swan; 24, Bell; 25, Carlyle; 26, George; 27, Tyson; 28, Tilton; 29, Sans Chambre; 30, Fraleck; 31, Pedro; 32, Attele; 33, Whitepine; 34, Pigeon; 35, Alphretta; 36, Joe; 37, Laura; 38, Whitson; 39, Hanmer; 40, Frenchmen; 41, Nelson; 42, Kukagami; 43, Horseshoe; 44, S. E. Baby; 45, Adelaide; 46, Ashigami; 47, Page; 48, Labelle; 49, Stull; 50, Hannah; 51, Baby; 52, Raft; 53, Clarabelle; 54, Skill; 55, Ratter; 56, Sawhorse; 57, Middle; 58, Little Round; 59, Emerald; 60, East Fox; 61, McFarlane; 62, Robinson; 63, Wawashkesh; 64, Deer; 65, Fairbank; 66, Round; 67, Kakakiwaganda; 68, Richard; 69, Griffin; 70, Anderson; 71, Little Panache; 72, Lewis.

pH of currently acidic lakes was higher and metal concentrations were lower during preindustrial times.

Although present-day circumneutral and alkaline lakes contain diatom taxa that are indicators of high-pH waters, these lakes have also experienced changes in diatom taxa in the past (e.g. *A. minutissima* has increased and *Cyclotella comta* has declined in percent abundance in recent sediments), indicating that recent limnological changes have also occurred in these lakes.

The distribution of common chrysophytes in recent and bottom samples follows patterns similar to those observed for diatoms (Fig. 3). *Mallomonas crassisquama* and *M. pseudocoronata* were the two most common chrysophyte taxa in the preindustrial samples. *Mallomonas crassisquama* is a pH-indifferent taxon whereas *M. pseudocoronata* is more common in circumneutral to alkaline waters (Smol 1986; Dixit et al. 1989b). Although no specific distribution patterns were observed in preindustrial samples, the distribution of chrysophytes in recent sediments indicates that in low-pH lakes, scales of *Synura echinulata* (an acid water, metal-tolerant taxon) are common whereas in circumneutral and alkaline lakes, scales of *M. pseudocoronata*, *M. caudata*, and *Synura petersenii* are frequently encountered. We did not plot the data for *Mallomonas hindonii* because it did not meet our selection criterion (i.e. 5% or more in at least five lakes) for inclusion in Fig. 3. However, it is interesting to note that this taxon was only found in the recent sediments of acidic lakes that have high lake water [Al] and low [Cu] and [Ni]. *Mallomonas hindonii* has previously been identified as an excellent indicator of low pH and high [Al] (Gibson et al. 1987; Cumming 1991).

TABLE 1. Calibration statistics for the diatom-inferred pH, [Al], [Ni], conductance, and [Ca] and chrysophyte-inferred pH models. Models for [Al], [Ni], conductance, and [Ca] were developed using $\log_e$ values (for details, see Dixit et al. 1991). The inferred data for these variables were back-transformed in this study. RMSE = root mean squared error.

Model	r^2	RMSE
Diatom-inferred		
pH	0.78	0.50
$\log_e$ Al (μg/L)	0.54	0.83
$\log_e$ Ni (μg/L)	0.64	1.03
$\log_e$ conductance (μS/cm)	0.71	0.41
$\log_e$ Ca (mg/L)	0.73	0.33
Chrysophyte-inferred		
pH	0.75	0.53

No scales of *M. hindonii* were found in any of the preindustrial sediments.

Inferred Limnological Changes

Diatom-inferred pH, [Al], [Ni], conductance, and [Ca] values were computed for the top and bottom samples, and differences (increase or decrease) between top and bottom samples are plotted in Fig. 4 and 5. As we discussed in our diatom calibration study (Dixit et al. 1991), we believe that our pH inferences are robust and can be considered on an absolute scale whereas inferences for [Al], [Ni], conductance, and [Ca] are less robust and should only be used to identify overall trends.

The diatom-inferred changes in pH show that, with the exception of a minor increase (0.02 pH) in Emerald Lake (No. 14), all lakes (28 in total) that have current measured lake water pH $\leq$ 6.02 have acidified. The inferred decline in pH of these lakes has ranged between 0.01 to 1.79 pH units. Lakes (22 in total) that have current measured pH between 6.02 and 6.97 have either decreased or increased in pH whereas, with the exception of one lake (No. 59), all 20 lakes that have measured pH $\geq$ 6.97 have become more alkaline in the Sudbury region. We recognize that, due to post-1970s reductions in SO_2 emissions, the pH of some Sudbury lakes has recently recovered (Keller et al. 1986; Gunn and Keller 1990), and it is therefore possible that we may be underestimating the extent of acidification in some Sudbury lakes (i.e. in some lakes the top sediment samples already represent the period of recent recovery). Similarly, some lakes (e.g. Hannah (No. 50) and Middle (No. 57)) were limed in the 1970s.

Although the chrysophyte-inferred pH change data (Fig. 6) support our diatom inferences, there are two marked differences. Similar to diatoms, chrysophyte data indicate that low-pH lakes (pH < 6.0) have acidified; however, the magnitude of the chrysophyte-inferred pH decline is generally greater. In a similar study in the Adirondack Park, Cumming et al. (1992) also observed that, in low-pH lakes, chrysophyte data indicate greater acidification than diatoms. The most plausible cause for this difference may be associated with the habitat and seasonality of chrysophytes. Because scaled chrysophytes are exclusively euplanktonic and bloom in the spring, when acidification from snowmelt is highest, we would expect these indicators to

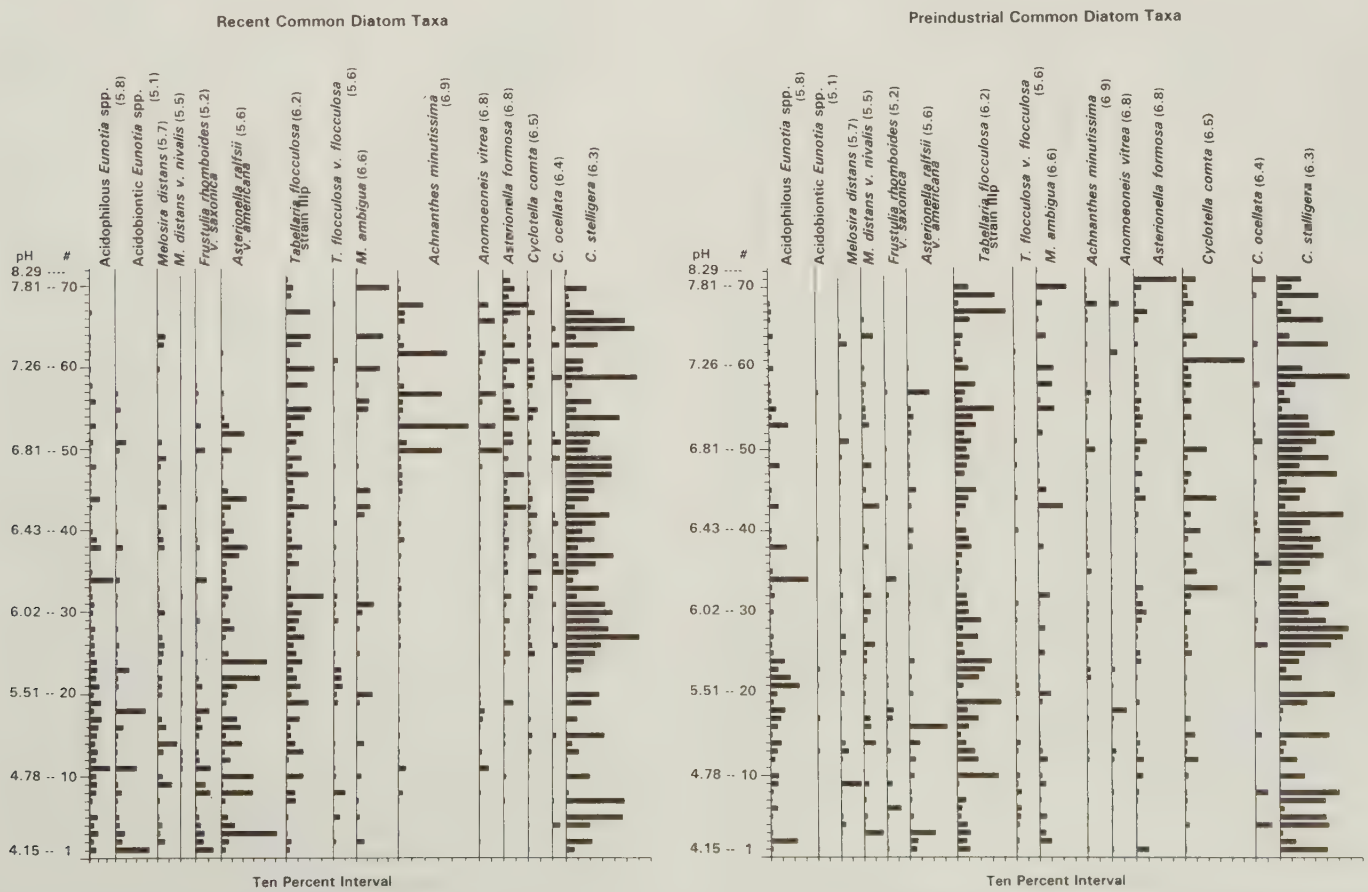

FIG. 2. Percent distribution of common diatom taxa in recent (tops) and preindustrial (bottoms) sediment samples. The lakes are ranked according to present-day measured lake water pH (Dixit et al. 1989b).

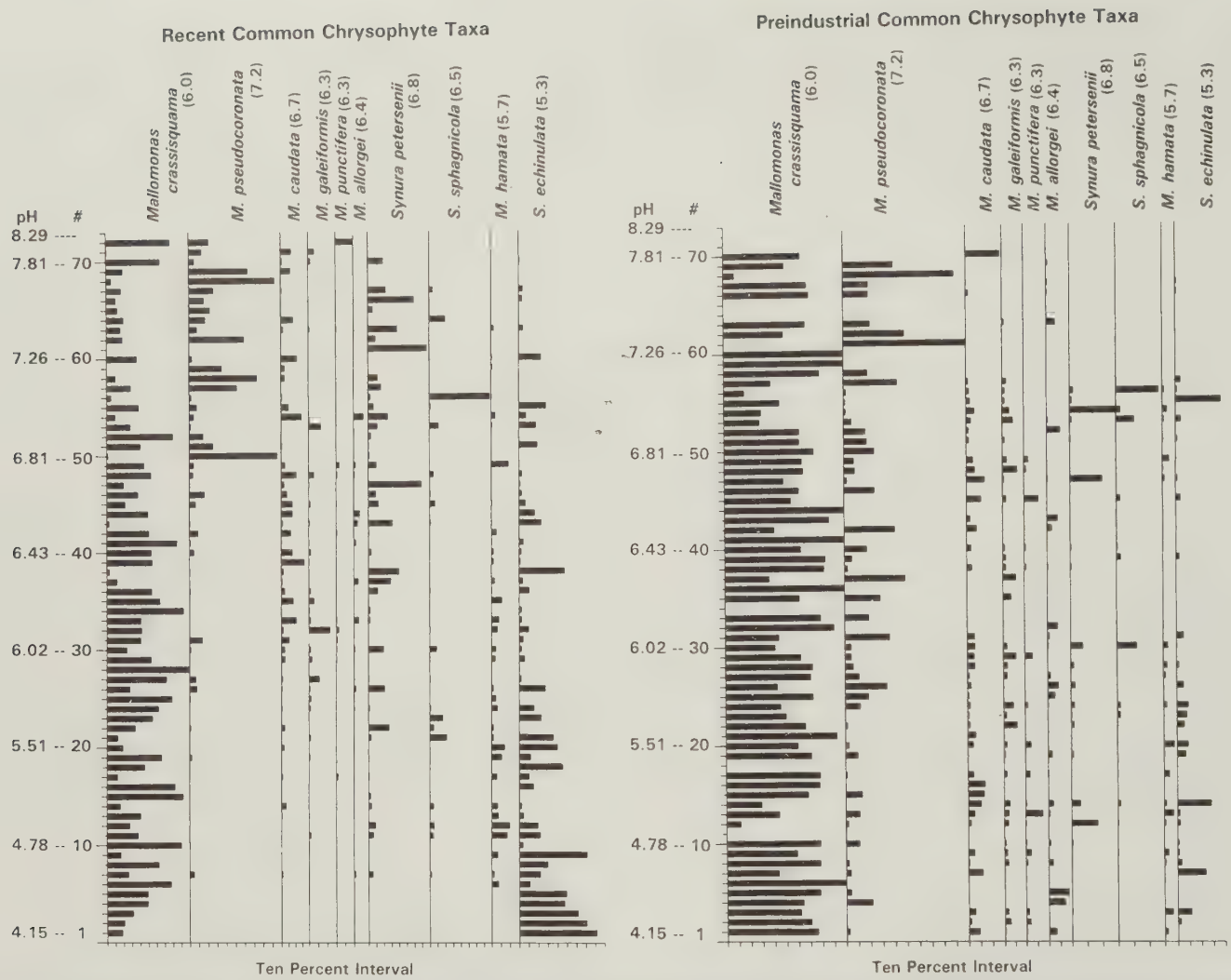

FIG. 3. Percent distribution of common chrysophyte taxa in recent (tops) and preindustrial (bottoms) sediment samples. The lakes are ranked according to present-day measured lake water pH (Dixit et al. 1989b).

infer greater acidification than diatoms. In fact, when analyzing continuous diatom and chrysophyte stratigraphic records from acidic lakes (e.g. Lumsden, George, and Acid; see Dixit et al. 1992b), we have also shown that chrysophytes indicate greater acidification than diatoms. Similar observations have been reported by Charles and Smol (1988), Davis et al. (1990), Cumming (1991), and Sullivan et al. (1992).

In circumneutral and alkaline lakes, chrysophytes indicate only small increases in pH (Fig. 6). Cumming et al. (1992) reported similar observations from more alkaline Adirondack lakes. It is possible that in high-pH lakes, chrysophytes are less sensitive indicators of environmental change. However, in poorly buffered waters, chrysophytes are generally present in high abundance and have been shown to be early warning indicators of changes in lake water quality (Smol 1986; Dixit et al. 1989a; Cumming 1991; Dixit et al. 1992a). Although the chrysophyte-inferred pH trend is not strong for high-pH lakes, our diatom-inferred pH data, long-term monitoring data in Sudbury (Gunn and Keller 1990), and modelling data from the Adirondacks (Sullivan et al. 1990) all suggest that the pH of alkaline lakes has indeed increased as a result of acid precipitation.

Many factors may be responsible for the alkalization of high-pH Sudbury lakes, such as (i) biogeochemical processes related to nitrate uptake by plants and sulphate reduction by bacteria (Kilham 1982; Cook et al. 1986), (ii) increased carbonate weathering in the watershed (Kilham 1982), (iii) watershed disturbances which tend to increase acid-neutralization capacity (Haines and Akielaszek 1983; Eilers et al. 1989), (iv) algal assimilation of NO_3^- and bacterial NO_3^- reduction (denitrification), which generates acid-neutralization capacity (Sullivan 1990), and (v) acid-neutralizing capacity generating sulphate reductions occurring in alkaline watersheds (Asbury et al. 1989).

In addition to recent recoveries in lake water pH in low-pH lakes around Sudbury, Gunn and Keller (1990), by comparing the pH readings taken in 1980 and 1987, also observed recent pH increases in circumneutral and alkaline lakes. They believed that these pH increases were due to post-1970 reductions in SO_2 emissions in the Sudbury region. Although our study supports their observations, we further suggest that the pH of alkaline lakes has been gradually increasing during this century as a result of acidic precipitation and other cultural activities in the region (possible mechanisms discussed above). Similar pH increases recorded in alkaline lakes from the Adirondacks (Cumming et al. 1992) and Maine (Kahl et al. 1992) further support our hypothesis. However, we realize that our top and bottom sediment study cannot identify the timing of the pH changes, as this would require detailed stratigraphic analyses.

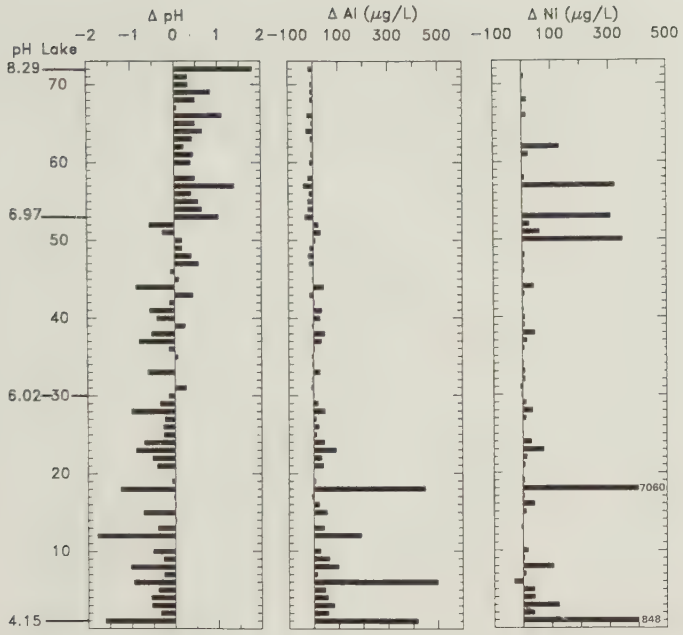

FIG. 4. Diatom-inferred estimates of historical changes (preindustrial to present) in lake water pH, total [Al], and [Ni] in the study lakes. Measured lake water pH values (Dixit et al. 1989b) are given on the left.

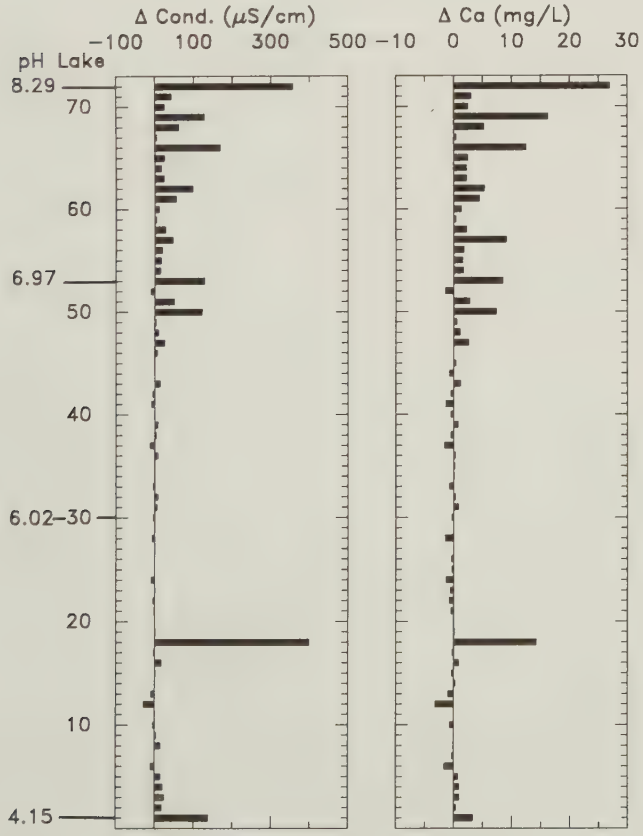

FIG. 5. Diatom-inferred estimates of historical changes (preindustrial to present) in lake water conductance and [Ca] in the study lakes. Measured lake water pH values (Dixit et al. 1989b) are given on the left.

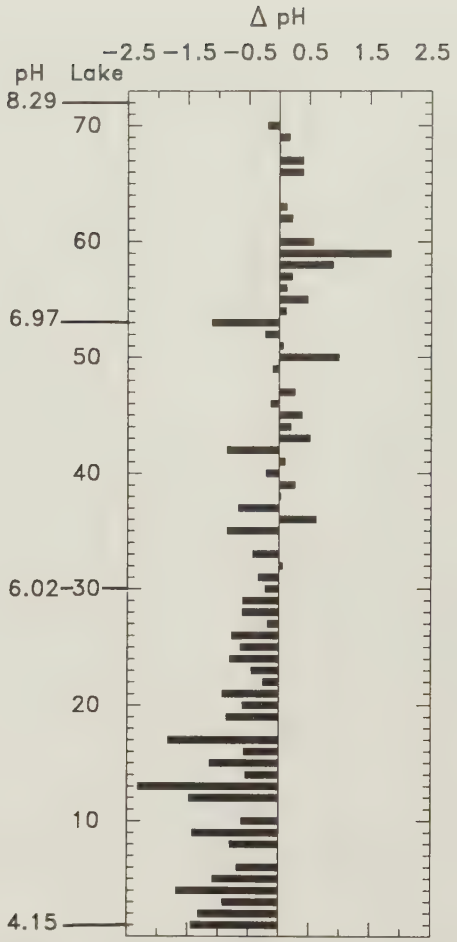

FIG. 6. Chrysophyte-inferred estimates of historical changes (preindustrial to present) in lake water pH in the study lakes. Measured lake water pH values (Dixit et al. 1989b) are given on the left.

In our ongoing research, we are analyzing additional sediment intervals of dated cores from more alkaline study lakes to clarify the timing and rates of limnological change in these lakes.

Diatom-inferred [Al] increased in most of the lakes that are presently acidic (pH ≤ 6.02); however, in other lakes, inferred [Al] has either slightly increased or decreased. The increase of [Al] in low-pH lakes is likely due to increased Al mobilization from the watershed and lake sediments (Cronan and Schofield 1979). On the other hand, the increase in inferred [Ni] in almost all our study lakes (Fig. 4) suggests that the [Ni] increases are independent of the changes in lake water pH (Fig. 4 and 6). The lakes for which we infer higher Ni inputs are generally located closer to smelters and/or mine tailing ponds. The lack of a relationship between [Al] and [Ni] changes is expected because Ni inputs were mainly atmospheric whereas Al inputs were from the mobilization of Al from the watershed and lake sediments. Stratigraphic inferences of [Ni] and [Al] for Sudbury lakes also confirm these observations (Dixit et al. 1992a, 1992b; Dixit et al. 1991). Geochemical analysis of our surface sediments also showed that sediment [Ni] is inversely related to the distance from the smelters (Palmer et al. 1989). As indicated by the surface sediment diatom calibration study of these lakes (Dixit et al. 1991), the lack of a relationship between changes in inferred pH and [Ni] further reinforces our belief that, to a certain extent, diatom assemblages respond independently to pH and metals, even if these variables are correlated.

Although inferred conductance has declined slightly in 15 lakes, inferred conductance has generally increased in the study region (Fig. 5). The maximum increase occurred in lake No. 18, which has received mine tailings in the past. Our data suggest that, in general, ion concentrations have increased in Sudbury lakes since industrial activity began in the region. However, in other regions, lake water ion concentrations have declined in recently acidified lakes (Sullivan et al. 1990), and Dixit et al. (1991) inferred modest decline in lake water conductance in a lake located 56 km northeast of Sudbury. In a few acidic lakes (Nos. 1–5), inferred conductance has increased; but these lakes are located close to the smelters, and thus receive high metal inputs. Moreover, these lakes also receive high ion loadings from their drainage basins because extensive degradation and vegetation loss have occurred in their watersheds (Gorham and Gordon 1960). In these acidic lakes, the increase in inferred [Ca] (Fig. 5) also suggests ion inputs from the watershed and sediments. In circumneutral and alkaline lakes, the large increases in inferred conductance and [Ca] indicate that, concomitant with acid precipitation and other cultural activity, ion leaching has increased from well-buffered watersheds. Similarly, increases of [Ca] in Muskoka–Haliburton lakes have been attributed to the deposition of strong acids (Harvey et al. 1981). Initially it was believed that, in response to increased sulphate deposition, concentrations of only H^+, Al, and HCO_3 change (Henriksen 1979); however, subsequent observations from Norwegian (Henriksen 1982) and North American (Wright 1983) lakes have indicated that increased base cation release (primarily Ca and Mg) accounted for up to 40% of added sulphate (Sullivan et al. 1990).

Temporal and Spatial Patterns in Lake Water pH

To examine temporal and spatial patterns in lake water pH, we grouped our lakes into five pH categories and developed a distribution map for change in diatom-inferred pH (Fig. 7). Study of this map graphically represents the changes in lake water pH that have occurred as a result of anthropogenic activity. In comparison with preindustrial times, the percentage of lakes whose present inferred pH is less than 5.5 has increased greatly (Table 2). Most of these lakes also experienced large increases of [Al] (Fig. 4). The percentage of lakes with inferred pH < 5.0 has increased from 1.4% in preindustrial times to 8.3% in the recent samples (Table 2). Similarly, for the pH range 5.0–5.5, the percentage of lakes has increased from 7% (preindustrial) to 20.8% (recent). The percentage of lakes in the pH range 5.5–6.0 has remained essentially the same at 18%. In the pH range 6.0–7.0, the percentage of lakes has declined from 63.4% (preindustrial) to 30.6% (recent) whereas in the pH category >7.0 the percentage of lakes has increased from 9.9% (preindustrial) to 22.2% (recent).

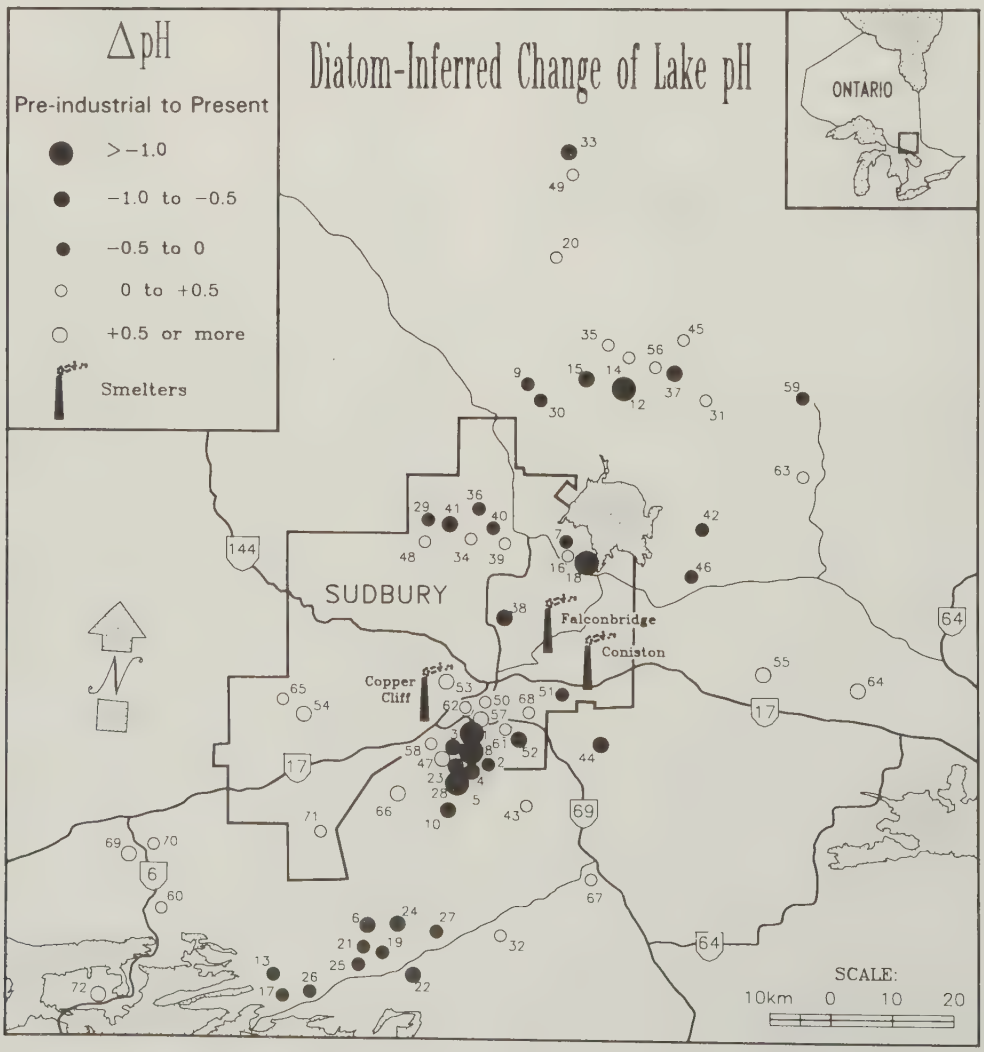

FIG. 7. Map showing diatom-inferred pH changes in the study lakes since preindustrial times.

TABLE 2. Percentage of lakes in five pH categories for preindustrial and recent times. These percentages were computed on the basis of diatom-inferred pH of the top (recent) and bottom (preindustrial) samples of the study lakes. The results presented here summarize how the percentages of lakes in each of five cateogries have changed since the preindustrial times.

pH category	Recent	Preindustrial
<5.0	8.3	1.4
5.0–5.5	20.8	7.0
5.5–6.0	18.1	18.3
6.0–7.0	30.6	63.4
>7.0	22.2	9.9

TABLE 3. Number and percentage of lakes in five diatom-inferred pH change categories. These data are based on diatom-inferred pH change between recent (tops) and preindustrial (bottoms) samples. The results presented here summarize the extent to which the lakes may have changed in the Sudbury region due to anthropogenic activity.

pH change	Number of lakes	Percentage of lakes
< -1.0	5	7.0
-1.0 to -0.5	14	19.7
-0.5 to 0	19	26.8
>0.0 to 0.5	24	33.8
>0.5	9	12.7

The most acidic lake during preindustrial times was Ruth-Roy Lake (No. 6; inferred pH = 4.9), located in Killarney Park. This is not surprising, as this lake drains quartzite ridges with almost no soil covering. Limnological data (Dixit et al. 1989b) suggest that Ruth-Roy is still the most acidic (pH 4.58) lake and contains the highest [Al] (511 μg/L) among our 11 Killarney Park lakes (Nos. 6, 13, 17, 19, 21, 22, 24, 26, 27, and 32). The lake has no fish community (Polkinghorne and Gunn 1981). Although the lake was naturally acidic, the inferred pH change data (Fig. 4 and 7) show that the lake has become even more acidic due to acid precipitation. Diatom-inferred [Al] data (Fig. 4) indicate that the lake has experienced the largest increase in [Al] of all the study lakes. In the top sediment of Ruth-Roy, the dominant diatom taxon was *Fragilaria acidobiontica* (66% of the total diatom sum) whereas in the bottom sediment this taxon was absent. *Fragilaria acidobiontica* is an excellent indicator of acidic and high-[Al] waters (Charles 1986). Similar results were obtained for our strongest chrysophyte indicator of acidic, high-[Al] waters; *M. hindonii*.

In addition to Ruth-Roy, there are six other naturally acidic (pH < 5.6) lakes (Nos. 3, 9, 14, 16, 17, and 18) in our data set. All these lakes are less than 25 ha in size and, with the exception of Lumsden Lake (No. 17; maximum depth 22 m), are all less than 10 m deep. Diatom species data (Fig. 2) indicate that acid water diatoms were common in these lakes even during preindustrial times; however, their abundances have further increased in the recent sediments.

Nineteen (27%) of our lakes had inferred pH ≤ 6.0 during preindustrial times (Table 2). This statement is inconsistent with current Ontario Ministry of the Environment guidelines which categorize lakes as "damaged" if their water pH is below 6.0 (Neary et al. 1990) and suggests that the Ministry's threshold pH is too high. Alternatively, one could argue that some Sudbury lakes are somehow atypical and should not be considered "reference" sites for other areas in Ontario. Finally, it is possible that there is some error in our inferences, but we point out that when compared with long-term water chemistry data in several Sudbury lakes, we have correctly inferred past lake water pH (Dixit et al. 1987, 1989a; Dixit et al. 1992a; Dixit et al. 1991).

The extent of diatom-inferred pH changes in our study lakes (Fig. 7) and the number and percentage of lakes falling into one of the five pH categories (Table 3) provides strong evidence that, as a result of anthropogenic activity, both acidification and alkalization have occurred in the Sudbury region. Although it has been widely accepted that widespread acidification has occurred in Sudbury lakes, our study is the first to suggest that a small number of lakes were naturally acidic in the study area. Although maximum acidification has occurred in lakes that are near the smelters (i.e. a radius of 20 km), widespread acidification has also occurred in, for example, the Killarney Provincial Park lakes located as far away as 60 km southwest from Sudbury. The timing and magnitude of acidification in the Killarney lakes are presented in Dixit et al. (1992b).

In the Sudbury region, it is common to find an alkaline lake (Fig. 1) in close proximity to a recently acidified lake (e.g. Nos. 1 and 61; Nos. 3 and 47). These data suggest that, due to pockets of carbonate-rich deposits in some watersheds, there are many lakes in and around Sudbury that have been able to maintain a high pH, and, in fact, inferred pH has increased in these lakes, in spite of heavy sulphate deposition.

Conclusions

Our paleolimnological study confirms that widespread acidification has occurred in lakes around Sudbury. In general, the presently most acidic lakes have acidified the most, but other factors such as geographic location with respect to prevailing wind patterns, the distance from smelters, and the local geology are important in determining the extent of acidification. In general, ion concentrations (inferred conductance and [Ca]) have increased in the majority of lakes. Although all the lakes have experienced increased input of atmospherically deposited metals (e.g. Ni), Al increases were especially prominent in the recently acidified lakes. The study is the first to show that pH has increased in alkaline Sudbury lakes since preindustrial times. The study clearly identifies that diatom and chrysophyte inferences from the top and bottom samples of short sediment cores from a large number of lakes can provide useful regional assessments of environmental change.

Acknowledgements

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References

ASBURY, C. E., F. A. VERTUCCI, M. D. MATTSON, AND G. E. LIKENS. 1989. Acidification of Adirondack lakes. Environ. Sci. Technol. 23: 362–365.

BATTARBEE, R. W. 1973. A new method for the estimation of absolute microfossil numbers, with special reference to diatoms. Limnol. Oceanogr. 18: 647–653.

BATTARBEE, R. W., J. MASON, I. RENBERG, AND J. F. TALLING [ED.] 1990. Palaeolimnology and lake acidification. The Royal Society, London. 445 p.

BEAMISH, J., AND H. H. HARVEY. 1972. Acidification of La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BIRKS, H. J. B., S. JUGGINS, AND J. M. LINE. 1990a. Lake surface-water chemistry reconstructions from palaeolimnological data, p. 301–313. *In* J. J.

Mason [ed.] The surface water acidification programme. Cambridge University Press, Cambridge.

BIRKS, H. J. B., J. M. LINE, S. JUGGINS, A. C. STEVENSON, AND C. J. F. TER BRAAK. 1990b. Diatoms and pH reconstructions. Philos. Trans. R. Soc. Lond. Ser. B 327: 263–278.

CHARLES, D. F. 1986. A new diatom species, *Fragilaria acidobiontica*, from acidic lakes in northeastern North America, p. 35–44. *In* J. P. Smol, R. W. Battarbee, R. B. Davis, and J. Meriläinen [ed.] Diatoms and lake acidity. Dr. W. Junk, Dordecht, The Netherlands.

CHARLES, D. F., R. W. BATTARBEE, I. RENBERG, H. VAN DAM, AND J. P. SMOL. 1989. Paleoecological analysis of diatoms and chrysophytes for reconstructing lake acidification trends in North America and Europe, p. 207–276. *In* S. A. Norton, S. E. Lindberg, and A. L. Page [ed.] Acid precipitation. Vol. 4. Soils, aquatic processes and lake acidification. Springer-Verlag, New York, NY.

CHARLES, D. F., AND J. P. SMOL. 1988. New methods for using diatoms and chrysophytes to reconstruct past lakewater pH. Limnol. Oceanogr. 33: 1451–1462.

1990. The PIRLA II Project: regional assessment of lake acidification trends. Verh. Int. Ver. Limnol. 24: 474–480.

COOK, R. B., C. A. KELLY, D. W. SCHINDLER, AND M. A. TURNER 1986. Mechanisms of hydrogen ion neutralization in an experimentally acidified lake. Limnol. Oceanogr. 31: 134–148.

CRONAN, C. S., AND C. L. SCHOFIELD. 1979. Aluminium leaching response to acid precipitation: effects on high-elevation watersheds in the northeast. Science (Wash., DC) 204: 304–306.

CUMMING, B. F. 1991. Paleoecological assessment of changes in Adirondack lakewater chemistry: historical (pre-1850) and recent (post-1970) trends. Ph.D. thesis, Queen's University, Kingston, Ont.

CUMMING, B. F., J. P. SMOL, J. C. KINGSTON, D. F. CHARLES, H. J. B. BIRKS, K. E. CAMBURN, S. S. DIXIT, A. J. UUTALA, AND A. R. SELLE. 1992. How much acidification has occurred in Adirondack region lakes (New York, USA) since preindustrial times? Can. J. Fish. Aquat. Sci. 49: 128–141.

DAVIS, R. B., D. S. ANDERSON, M. C. WHITING, J. P. SMOL., AND S. S. DIXIT. 1990. Alkalinity and pH of three lakes in northern New England, U.S.A., over the past 300 years. Philos. Trans. R. Soc. Lond. B 327: 413–421.

DICKMAN, M., AND S. S. RAO. 1989. Diatom stratigraphy in acid-stressed lakes in the Netherlands, Canada, and China, p. 115–143. *In* S. S. Rao [ed.] Acid stress and aquatic microbial interactions. CRC Press, Inc., Boca Raton, FL.

DILLON, P. J., R. A. REID, AND R. GIRARD. 1986. Changes in the chemistry of lakes near Sudbury, Ontario following reductions of SO_2 emissions. Water Air Soil Pollut. 31: 59–65.

DIXIT, A. S., S. S. DIXIT, AND J. P. SMOL. 1992a. Algal microfossils provide high temporal resolution of environmental trends. Water Air Soil Poll. 62: 75–87.

1992b. Long-term trends in lake water pH and metal concentrations inferred from diatoms and chrysophytes in three lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 17–24.

DIXIT, S. S. 1986. Algal microfossils and geochemical reconstructions of Sudbury lakes: a test of the paleo-indicator potential of diatoms and chrysophytes. Ph.D. thesis, Queen's University, Kingston, Ont. 190 p.

DIXIT, S. S., A. S. DIXIT, AND R. D. EVANS. 1987. Paleolimnological evidence of recent acidification in two Sudbury (Canada) lakes. Sci. Total Environ. 67: 53–67.

DIXIT, S. S., A. S. DIXIT, AND J. P. SMOL. 1989a. Lake acidification recovery can be monitored using chrysophycean microfossils. Can. J. Fish. Aquat. Sci. 46: 1309–1312.

1989b. Relationship between chrysophyte assemblages and environmental variables in seventy-two Sudbury lakes as examined by canonical correspondence analysis (CCA). Can. J. Fish. Aquat. Sci. 46: 1667–1676.

1991. Multivariable environmental inferences based on diatom assemblages from Sudbury (Canada) lakes. Freshwater Biol. 26: 251–266.

DIXIT, S. S., J. P. SMOL, J. C. KINGSTON, AND D. F. CHARLES. 1992. Diatoms: powerful indicators of environmental change. Environ. Sci. Technol. 26: 22–33.

EILERS, J. M., G. E. GLASS, A. K. POLLACK, AND J. A. SORENSEN. 1989. Changes in conductivity, alkalinity, calcium, and pH during a fifty-year period in selected northern Wisconsin lakes. Can. J. Fish Aquat. Sci. 46: 1929–1944.

GIBSON, K. A., J. P. SMOL, AND J. FORD. 1987. Chrysophycean microfossils provide new insight into the recent history of a naturally acidic lake (Cone Pond, New Hampshire). Can. J. Fish. Aquat. Sci. 44: 1584–1588.

GLEW, J. R. 1988. A portable extruding device for close interval sectioning of unconsolidated core samples. J. Paleolimnol. 1: 235–239.

GORHAM, E., AND A. G. GORDON. 1960. The influence of smelter fumes upon the chemical composition of lake waters near Sudbury, Ontario, and upon the surrounding vegetation. Can. J. Bot. 38: 477–487.

GUNN, J. M., AND W. KELLER. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

HAINES, T. A., AND J. J. AKIELASZEK. 1983. A regional survey of the chemistry of headwater lakes and streams in New England. U.S. Fish Wildl. Serv. FWS/OBS-80 No. 15: 141 p.

HARVEY, H. H., R. C. PIERCE, P. J. DILLON, J. R. KRAMER, AND D. M. WHELPDALE. 1981. Acidification of the Canadian aquatic environment: scientific criterion for assessment of the effects of acidic deposition on aquatic ecosystems. Natl. Res. Counc. Can. Rep. No. 18475. National Research Council of Canada, Ottawa, Ont.

HENRIKSEN, A. 1979. A simple approach for identifying and measuring acidification of freshwater. Nature (Lond.) 278: 542–545.

1982. Changes in base cation concentrations due to freshwater acidification. Acid rain Research Report, Norwegian Institute for Water Research, Oslo, Norway.

HOWARD-WHITE, F. B. 1963. Nickel, an historical review. Longmans, Toronto, Ont.

KAHL, J., T. A. HAINES, S. A. NORTON, AND R. B. DAVIS. 1992. Recent trends in the acid–base status of surface waters in Maine, USA. Water Air Soil Pollut. (In press)

KELLER, W., J. M. GUNN, AND N. D. YAN. 1992. Evidence of biological recovery of acid stressed lakes near Sudbury, Canada. Environ. Pollut. 78: 79–85.

KELLER, W., J. R. PITBALDO, AND N. I. CONROY. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. Water Air Soil Pollut. 31: 774–775.

KILHAM, P. 1982. Acid precipitation: its role in the alkalization of a lake in Michigan. Limnol. Oceanogr. 27: 856–867.

KINGSTON, J. C., AND H. J. B. BIRKS. 1990. Dissolved organic carbon reconstructions from diatom assemblages in PIRLA project lakes, North America. Philos. Trans. R. Soc. Lond. Ser. B 327: 279–288.

LINE, J. M., AND H. J. B. BIRKS. 1990. WACALIB version 2.1 — a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging. J. Paleolimnol. 3: 170–173.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ontario Ministry of the Environment Report, Dorset, Ont.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1984. Monitoring of northeastern Ontario lakes, 1981–1983. Ontario Ministry of the Environment Technical Report.

PALMER, G. R., S. S. DIXIT, J. D. MACARTHUR, AND J. P. SMOL. 1989. Elemental analysis of lake sediment from Sudbury, Canada, using particle-induced X-ray emission. Sci. Total Environ. 87/88:141–156.

POLKINGHORNE, D., AND J. GUNN. 1981. Sudbury district lake trout lakes: a description of the lakes and the changes produced by man. Ontario Ministry of Natural Resources Report, Sudbury District.

SMOL, J. P. 1986. Chrysophycean microfossils as indicators of lakewater pH, p. 275–287. *In* J. P. Smol, R. W. Battarbee, R. B. Davis, and J. Meriläinen [ed.] Diatoms and lake acidity. Dr. W. Junk, Dordecht, The Netherlands.

SULLIVAN, T. J. 1990. Historical changes in surface water acid–base chemistry in response to acidic deposition. State-of-Science/Technology Report 11, National Acid Precipitation Assessment Program, Washington, DC.

SULLIVAN, T. J., D. F. CHARLES, J. P. SMOL, B. F. CUMMING, A. R. SELLE, D. THOMAS, J. A. BERNETT, AND S. S. DIXIT. 1990. Quantification of changes in lakewater chemistry in response to acidic deposition. Nature (Lond.) 345: 54–58.

SULLIVAN, T. J., R. S. TURNER, D. F. CHARLES, B. F. CUMMING, J. P. SMOL, C. L. SCHOFIELD, C. T. DRISCOLL, B. J. COSBY, H. J. B. BIRKS, A. J. UUTALA, J. C.KINGSTON, S. S. DIXIT, J. A. BERNETT, P. F. RYAN, AND D. R. MARMOREK. 1992. Use of historical assessment for evaluation of process-based model projections of future environmental change: lake acidification in the Adirondack Mountains, New York, U.S.A. Environ. Pollut. 77: 253–262.

TER BRAAK, C. J. F., AND H. VAN DAM. 1989. Inferring pH from diatoms: a comparison of old and new calibration methods. Hydrobiologia 178: 209–223.

WRIGHT, R. F. 1983. Predicting acidification of North American lakes. Acid Rain Research Report 3/1983, Norwegian Institute for Water Research, Oslo, Norway.

Long-Term Trends in Lake Water pH and Metal Concentrations Inferred from Diatoms and Chrysophytes in Three Lakes near Sudbury, Ontario

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Diatom valves and chrysophyte scales were analyzed in sediment cores to assess historical (post-1860) and recent (since 1970) trends in lake water pH, total [Al], and [Ni] in Lumsden, George, and Acid lakes (Killarney Provincial Park, Ontario). Although acidification in Lumsden and Acid lakes started in the 1930s, rapid acidification only occurred since the 1960s. As lake water pH declined, inferred [Al] greatly increased causing the extirpation of the sport fisheries. In nearby George Lake, acidification started in the 1920s, and inferred lake water pH declined about 0.5 of a pH unit by 1960. The fish community in George Lake survived where the inferred acidification was less severe than Acid and Lumsden lakes. As in previous paleolimnological studies, chrysophytes generally indicate earlier and more marked acidification trajectories when compared with trends inferred from diatoms, probably because the vernal blooming and euplanktonic chrysophytes are tracking spring pH depressions. Although all three lakes have acidified and metal concentrations have increased during this century, our study provides evidence that these lakes, located as far as 60 km away from Sudbury, are showing signs of biological and chemical recovery as a result of recent reductions in SO_2 emissions from the Sudbury smelters.

Les valves de diatomées et les écailles de chrysophytes ont été analysées dans des carottes de sédiments dans le but d'évaluer les tendances historiques (après 1860) et récentes (depuis 1970) en ce qui concerne le pH, la concentration d'Al total et la concentration de Ni dans l'eau des lacs Lumsden, George et Acid (dans le Parc provincial de Killarney (Ontario)). Même si l'acidification des lacs Lumsden et Acid a commencé dans les années 1930, l'acidification rapide ne date que des années 1960. Pendant que le pH de l'eau des lacs diminuait, la concentration d'Al estimée par inférence augmentait de manière considérable, causant la disparition des pêcheries de poisson gibier. Dans le lac Georges voisin, l'acidification a commencé dans les années 1920 et le pH de l'eau du lac estimé avait diminué d'environ 0,5 d'une unité de pH en 1960. L'ichtyofaune du lac George a survécu aux endroits où l'acidification estimée était moins prononcée que dans les lacs Acid et Lumsden. Comme dans les études paléolimnologiques précédentes, les chrysophytes indiquent généralement des processus d'acidification plus précoces et plus prononcés par comparaison avec les tendances déduites à partir des diatomées, probablement parce que la prolifération printanière et les chrysophytes euplanctoniques suivent les dépressions du pH au printemps. Même si les trois lacs se sont acidifiés et si leurs concentrations de métaux ont augmenté durant ce siècle, notre étude montre que ces lacs, situés jusqu'à 60 km de Sudbury, montrent des signes de récupération biologique et chimique à la suite des récentes réductions des émissions de SO_2 des fonderies du Sudbury.

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The acidification of poorly buffered lakes in the Sudbury region of Canada has been a major environmental concern because of the massive emissions of SO_2 and toxic metals from the smelters in Sudbury (Gorham and Gordon 1960; Beamish and Harvey 1972; Keller et al. 1986). Metal mining and smelting operations started in this region in the 1880s. Since the early 1970s, however, SO_2 emissions have declined by about 50% because of the closure of the Coniston Smelter in 1972, the installation of the tall stack in 1972 and improved abatement measures at the Copper Cliff Smelter, and reduced activity at the Falconbridge Smelter (Dillon et al. 1986; Keller et al. 1986; Gunn and Keller 1990). As an outcome of these changes, recent recovery in water quality has been reported in Sudbury lakes (Dillon et al. 1986; Hutchinson and Havas 1986; Gunn and Keller 1990). Paleolimnological evidence of recent recovery has also been documented in lakes located close to the smelters (Dixit et al. 1989a; Dixit et al. 1992).

Diatoms and chrysophytes have been used extensively to reconstruct lake water pH changes in acid-sensitive lakes (Charles et al. 1989; Dickman and Rao 1989; Battarbee et al. 1990; Birks et al. 1990b); however, recent studies have demonstrated that these algae can also be used to infer past lake water metal concentrations, although these inferences are not as robust as pH inferences (Birks et al. 1990a; Dixit et al. 1991; Cumming et al. 1992). The application of canonical correspondence analysis (ter Braak 1986) and weighted-averaging regression and calibration (ter Braak and van Dam 1989; Birks et al. 1990b) has improved our ability to develop predictive models based on algal fossils (Dixit et al. 1989b; Stevenson et al. 1989; Birks et al. 1990a, 1990b; Dixit et al. 1991).

The Killarney Provincial Park lakes in the La Cloche Mountains have been adversely affected by acid precipitation, and these lakes were amongst the first sites in Canada where damage to fish populations was attributed to acid rain (Beamish and Harvey 1972; Beamish and Van Loon 1977; Gunn and Keller 1980). Many lakes (e.g. Lumsden and Acid) supported good sport fisheries, such as for lake trout (*Salvelinus namaycush*), in the past (Harvey 1975). Although the fish population was declining in the 1960s, the pH measurements recorded for these lakes by the Ontario Department of Lands and Forests were unusually high (cited in Beamish and Harvey 1972). Because detailed limnological studies in this region were only initiated in the late 1960s and early 1970s, no reliable historical data are available to characterize the background or preindustrial limnological characteristics of the lakes. High Al concentrations, which are toxic to fish (Baker and Schofield 1980; Muniz and Leivestad 1980), have only been measured in the Killarney lakes since the 1980s (Hulsman et al. 1983; Bleiwas et al. 1984).

The objectives of our study are to (i) assess the postindustrial (since 1860) changes in lake water pH and metal concentrations in Lumsden, George, and Acid lakes (in Beamish and Harvey (1972), Acid Lake was referred to as Lumsden II), (ii) compare the inferred changes with the reported fish losses from the study lakes, and (iii) determine if these Killarney Provincial Park lakes are recovering, continuing to acidify, or are in steady state since the mid-1970s, when SO_2 emissions declined in the Sudbury basin.

Study Area and Study Lakes

Our three study lakes are located about 60 km southwest of Sudbury in Killarney Provincial Park (Fig. 1; Table 1). The park, located in the La Cloche Mountains, is a well-known tourist attraction, providing both summer and winter recreational activities. Our study area is on the Precambrian Shield and is dominated by quartzite with a discontinuous thin overburden consisting of sandy to silty till (Bleiwas et al. 1984). The lakes are very oligotrophic and the terrestrial vegetation ranges from deciduous to coniferous forests. Extensive logging occurred in and around the park area from the 1860s to the early 1900s (OMNR 1986). The study lakes are part of the 72-lake calibration set that we have sampled in the Sudbury region to develop diatom- and chrysophyte-based calibration models to infer acidity-related limnological changes (Dixit et al. 1989b; Dixit et al. 1991).

Materials and Methods

In July 1987, a short sediment core (~30 cm long) was obtained from the deep basin of each of the study lakes using a modified K-B gravity corer, especially designed to sample surface sediments. The cores were sectioned at close intervals using an extrusion device, similar to the one designed by Glew (1988). The surface 1 cm of the core was sectioned at 0.25-cm intervals, from 1 to 5 cm at 0.5-cm intervals, from 5 to 10 cm at 1-cm intervals, and the remainder of the core at 2-cm intervals. Sediment samples were digested using strong acids (Battarbee 1986), and the resulting slurry was evaporated onto coverglasses using the Battarbee (1973) method. From each interval, a minimum of 400 diatom valves and 400 chrysophyte scales were identified and counted at 1250× magnification. The cores were dated by measuring the ^{210}Pb activity in the sediment samples at the Chalk River Nuclear Laboratory, Chalk River, Ont. (Canada). The constant rate of supply (CRS) model was used to calculate the dates, using the computer program written by Binford (1990). We used weighted-averaging regression and calibration (Line and Birks 1990) to compute diatom-inferred pH, [Al], and [Ni] and chrysophyte-inferred pH for sedimentary assemblages (Dixit et al. 1989b; Dixit et al. 1991). Our diatom-based pH, Al, and Ni models use simple weighted-averaging with inverse deshrinking. The details on statistical significance in reconstructing these variables are presented in Dixit et al. (1991). The chrysophyte-inferred pH model is based on tolerance weighted-averaging with inverse deshrinking. The ecological optima of the taxa we report on below are detailed in Dixit et al. (1989b) and Dixit et al. (1991).

Results and Discussion

Lumsden Lake

Marked changes in diatom species composition have occurred in Lumsden Lake over the last century (Fig. 2A). The first shift occurred between the early 1930s and 1970s, when the relative abundance of *Asterionella ralfsii* v. *americana* increased dramatically. Between 1970 and 1980, this taxon was largely replaced by more acidic and metal-tolerant taxa, such

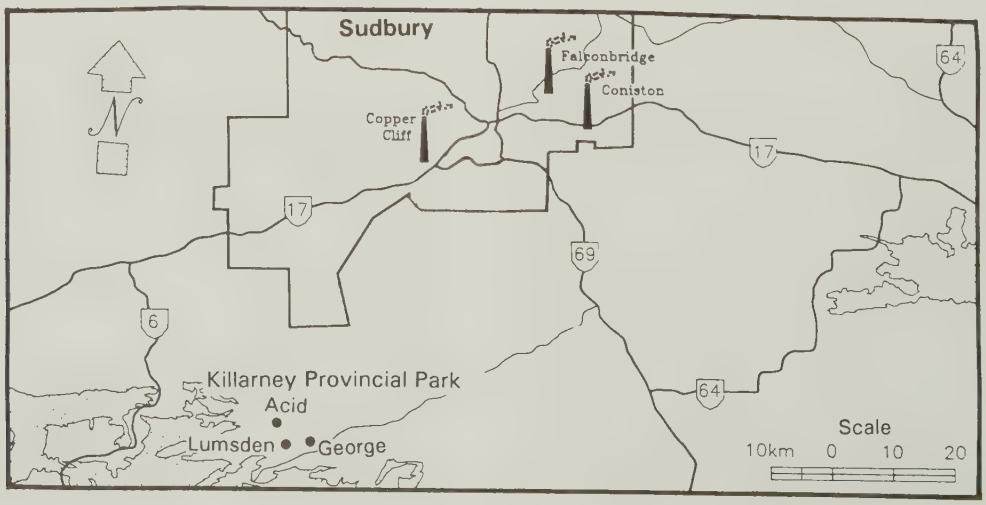

FIG. 1. Study area showing the location of the study lakes.

TABLE 1. Selected limnological characteristics of Lumsden, George, and Acid lakes, as measured in 1987 (Dixit et al. 1989a). Area, maximum depth, and mean depth data are from Harvey (1975) and Beamish and Van Loon (1977).

Variable	Lumsden	George	Acid
pH	5.09	5.73	4.92
Alkalinity (μeq/L)	−1.6	8.4	−7.8
Conductivity (μS/cm²)	24	31	26
Ni (μg/L)	38	4	7
Al (μg/L)	240	54	250
Total N (μg/L)	110	110	68
Total P (μg/L)	5	4	4
Secchi (m)	8.5	14	11.3
Area (ha)	22	148	18
Maximum depth (m)	22	35	19
Mean depth (m)	7	19	—
Coring depth (m)	17	22	14
Elevation (m)	238	186	315

as *Frustulia magaliesmontana*, *F. rhomboides* v. *saxonica*, *Eunotia exigua*, *Melosira distans*, *M. distans* v. *nivalis*, and *Navicula sublitissima*. Circumneutral and pH-indifferent taxa (i.e. *Cyclotella stelligera*, *C. comta*, and *Tabellaria flocculosa* strain IIIp) also declined during the 1970s.

The shift in diatom species between the 1930s and 1980s indicates that the lake was acidifying and metal concentrations were increasing. However, since about 1980, the relative abundance of *A. ralfsii* v. *americana*, *C. stelligera*, and *C. comta* had increased, and the more acidobiontic and metal-tolerant taxa have declined in abundance, which suggests a recent recovery in the lake.

Similar to diatoms, chrysophyte populations have also experienced distinct changes in the past (Fig. 3A). The first shift (since 1930s) was marked by an increase in the relative abundance of the acidic and metal-tolerant taxon *Synura echinulata*, followed by declines in *Mallomonas punctifera*, *M. crassisquama*, and *Chrysosphaerella*. *Mallomonas punctifera* is an indicator of circumneutral to alkaline waters and *M. crassisquama* is pH indifferent. In Sudbury lakes, *Chrysosphaerella* scales are frequently encountered in slightly acidic to circumneutral lakes. Between about 1975 and 1985, *Mallomonas hindonii* became the dominant scaled chrysophyte species in the lake. However, since then, *S. echinulata* and *M. hindonii* have declined, with a compensatory increase in the other common taxa (Fig. 3A). In this study, we have not distinguished *Mallomonas duerrschmidtiae*, a newly described species, from *M. crassisquama*. Although we recognize that these two taxa have different ecological distributions, it is unlikely that our interpretation will change greatly after we separate these two taxa because the majority of scales that we refer to as *M. crassisquama* are actually *M. duerrschmidtiae*.

The diatom- and chrysophyte-inferred pH profiles indicate that the lake's background pH ranged between 5.4 and 5.9 and that the chrysophyte-inferred pH values were generally about 0.5 of a pH unit higher than the diatom values (Fig. 4A). Chrysophyte-inferred pH indicates that acidification started in the 1930s and that by the mid-1960s, lake water pH had declined about 0.4 of a pH unit. Diatom inferences suggest that acidification started in the 1940s and that by 1960, lake water pH had declined only slightly. In other studies, we have also reported that chrysophytes often predate diatom-inferred acidification by 5–10 yr, and sometimes even longer (Smol 1986; Dixit et al. 1992). We believe that this is partially due to the fact that all the chrysophytes are euplanktonic and because

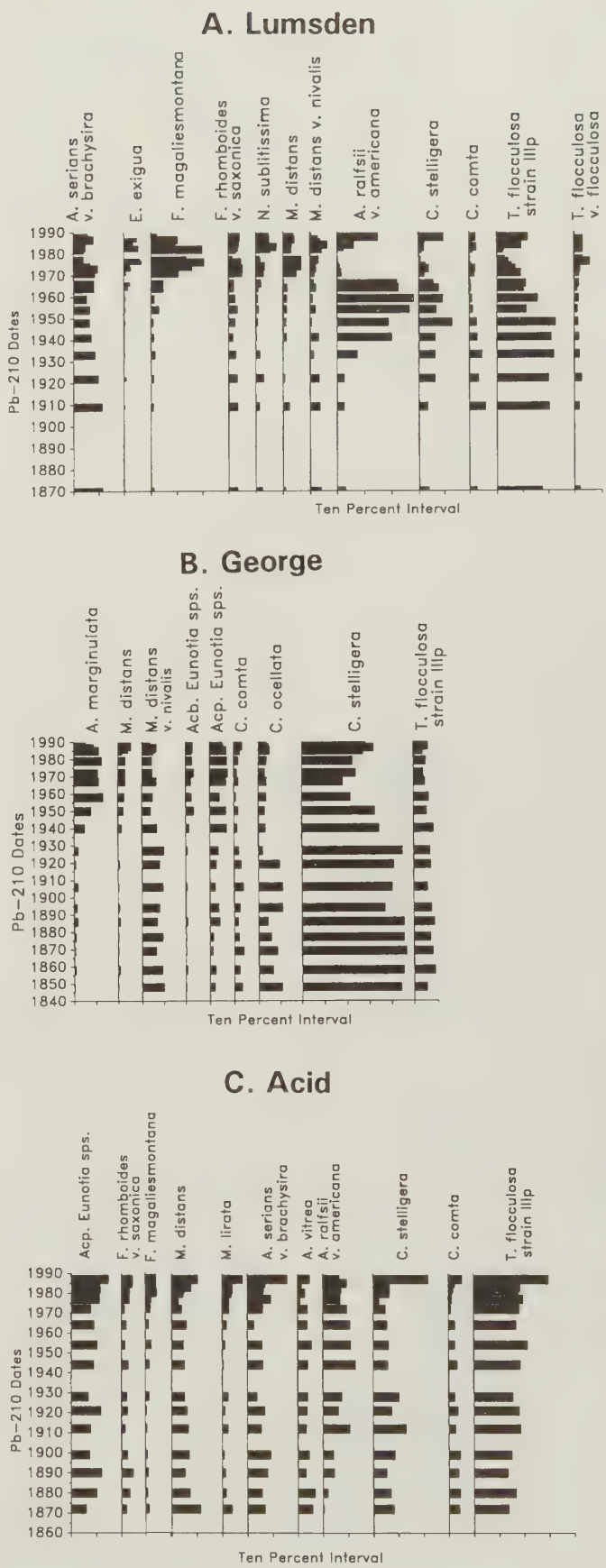

FIG. 2. Relative frequency diagram of the stratigraphic distribution of common diatom taxa from (A) Lumsden, (B) George, and (C) Acid lakes.

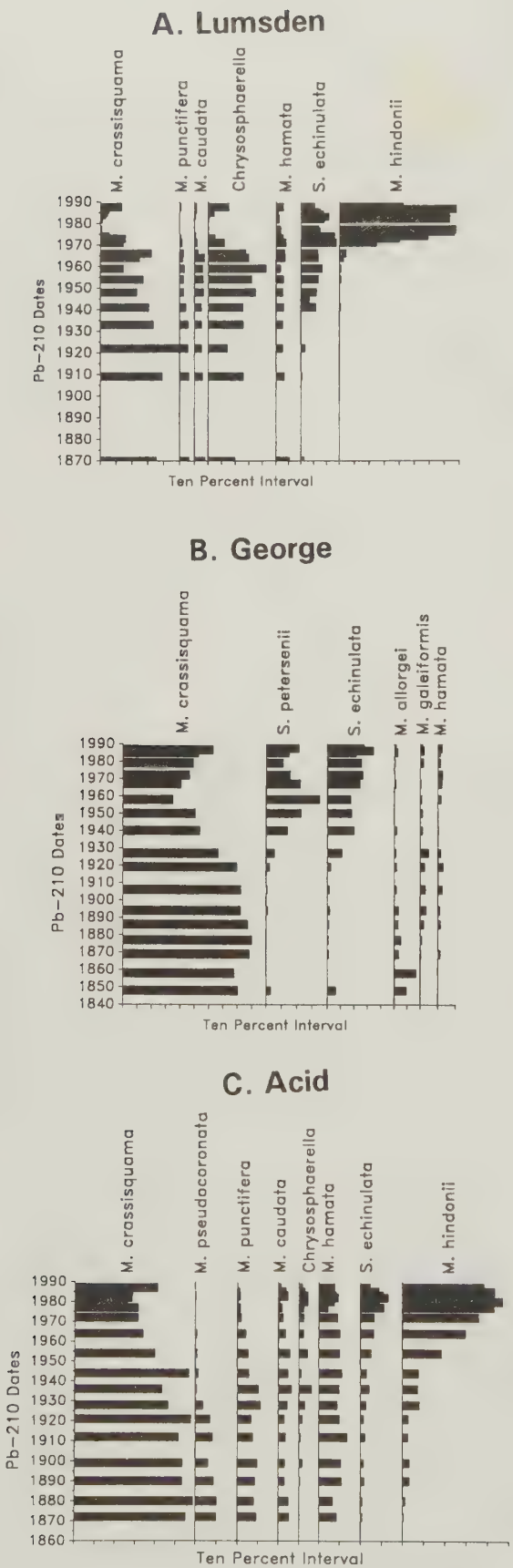

FIG. 3. Relative frequency diagram of the stratigraphic distribution of common chrysophyte taxa from (A) Lumsden, (B) George, and (C) Acid lakes.

most chrysophytes bloom in early spring, and so more closely track acid shock conditions. Both diatoms and chrysophytes show that maximum acidification occurred between the early 1960s and 1980. However, since the early 1980s, both diatoms and chrysophytes infer a marked pH recovery in lake water.

The difference of about 0.7 of a pH unit between diatom- and chrysophyte-inferred pH may be associated to a lag response in diatoms to a rapid decline in pH between about 1970 and 1980. Dixit et al. (1992) also found similar differences in one other Sudbury lake. Moreover, chrysophytes may infer lower pHs because they respond to early spring lake water chemistry when the lake water pH is generally lower and the [Al] are higher whereas diatoms infer average, ice-free condition. Measured lake water pHs for this lake include an average annual pH of 4.6 in 1969 (Beamish 1974), a pH of 4.4 in August 1971 (Beamish and Harvey 1972), and an average pH of 4.8 for 1972 and 1973. The measured lake water pHs for 1979–80 (Stokes and Yung 1986) are close to our diatom-inferred pHs for the early 1970s. The lowest measured pH (3.9) is very close to the chrysophyte-inferred pH (4.1) for that period whereas the maximum measured pH (4.8) value corresponds to the diatom-inferred pH (4.7). These data further indicate that chrysophyte assemblages may respond to spring depressions. The 6.8 pH value reported for 1961 by the Ontario Department of Lands and Forests (cited in Beamish and Harvey 1972) does not compare well with our inferred values, as our paleolimnological data suggest that, over the last 100 yr, the lake never had such a high pH. Possible analytical error may be responsible for this difference because the pH measurements by the Ontario Department of Lands and Forests were made colorimetrically. Similarly, pH measurements obtained for dilute waters in Adirondack lakes in the 1920s and 1930s were considered unreliable because of the use of colorimetric indicator solutions (Asbury et al. 1989). The measured lake water pH of 5.1 in 1987 is bracketed by our diatom-inferred pH (5.3) and chrysophyte-inferred pH (4.8) for the most recently deposited sediment.

The diatom-inferred Al profile indicates that lake water [Al] has greatly increased since about 1960 (Fig. 4B). Not surprisingly the timing of [Al] increase corresponds closely with the lake's acidification, and the highest inferred [Al] was recorded when the inferred pH was lowest. Since about 1980, inferred lake water [Al] has returned to pre-1950 levels. However, the 1987 measured [Al] (240 μg/L) is substantially higher than our inferred value (110 μg/L) for the surface sediment. The low inferred value for the surface sediment mimics our diatom calibration study, where we observed that in waters that have high [Al], our inferred [Al] model underestimates these high metal concentrations (Dixit et al. 1991). Nonetheless, we believe that it is possible to at least assess trends in [Al] using sedimentary diatom assemblages.

In acidified waters, Pillsbury and Kingston (1990) and Gensemer (1990) have shown a strong relationship between [Al] and the distribution of *A. ralfsii* v. *americana*, indicating its sensitivity to high [Al]. The shift in the relative abundance of *A. ralfsii* v. *americana* in Lumsden Lake appears to be closely related to the shift in pH and [Al]. When the lake was acidifying, the percent abundance of *A. ralfsii* v. *americana* increased dramatically because [Al] was still low at this time (as inferred by diatoms). However, as the lake became more acidic, [Al] increased and the relative abundance of *A. ralfsii* v. *americana* greatly declined. Since about 1980, when the lake water pH started to recover and [Al] declined, *A. ralfsii* v. *americana* once again increased in abundance (Fig. 2A).

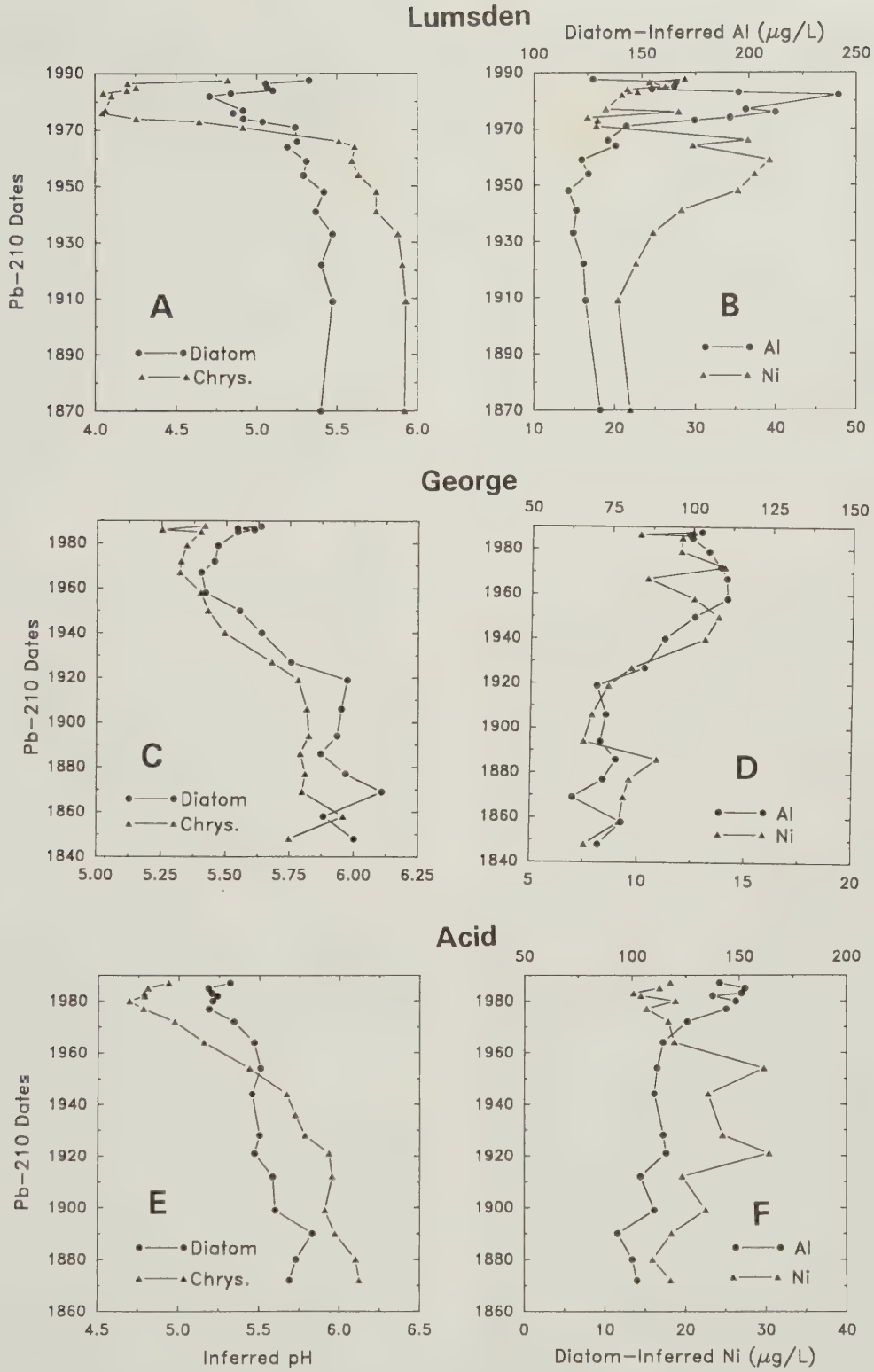

FIG. 4. Diatom- and chrysophyte-inferred pH reconstructions for (A) Lumsden, (C) George, and (E) Acid lakes and diatom-inferred [Al] and [Ni] reconstructions for (B) Lumsden, (D) George, and (F) Acid lakes.

During this century, diatom-inferred [Ni] has varied greatly (Fig. 4B). The inferred [Ni] started to increase about 1920 and peaked at about 1960, a time when metal mining and smelting was at its peak in Sudbury (Keller et al. 1986). The timing of the increase of Ni input to the lake coincides with the installation of stacks at the Sudbury smelters in the 1920s. Our inferred Ni increase predates the inferred increases in Al. This is not surprising, as the lake received Ni inputs mainly from the atmosphere, but the increased [Al] is mainly the result of increased mobilization of Al from the watershed and the sediments as acidification progressed. Similar observations have been reported by Dixit et al. (1991) for Chiniguchi Lake. A recovery in inferred [Ni] since about 1960 correlates with the decline in S and metal emissions in Sudbury. The diatom-

inferred [Ni] for the most recent sediment is close to the pre-1920 levels (about 22 μg/L). The measured lake water [Ni] in 1987 was 38 μg/L. The pre-1920 inferred [Ni] is higher than expected for preindustrial times. As we observed in our calibration study (Dixit et al. 1991), this is most likely because our Ni inference model overestimates [Ni] in low-Ni waters whereas estimations are lower for waters that have high [Ni]. These data suggest that, similar to inferred [Al], inferred [Ni] should only be used to estimate overall trends.

Beamish and Harvey (1972) reported that Lumsden Lake supported a viable lake trout fishery until 1965. The fish population decline correlates closely with the onset of rapid acidification and the resulting increase in lake water [Al] in the 1960s. The disappearance of lake trout in 1967 was followed by the extirpation of the slimy sculpin (*Cottus cognatus*) in 1967–68, white sucker (*Catostomus commersoni*) in 1968–69, and lake herring (*Coregonus artedi*) and trout-perch (*Percopsis omiscomaycus*) during 1967–70. Between 1960–61 and 1971 the number of fish species declined from eight to one (Harvey 1975).

George Lake

Diatom species composition has experienced two pronounced shifts in George Lake during this century (Fig. 2B). The first shift started in the 1920s when circumneutral, alkaliphilous, and pH-indifferent taxa (e.g. *Cyclotella ocellata, C. comta*, and *C. stelligera*) declined in abundance whereas more acidic taxa (e.g. *Achnanthes marginulata, M. distans,* and *Eunotia* species) gradually increased. The second shift occurred in the early 1970s when the relative abundance of alkaliphilous, circumneutral, and pH-indifferent diatoms increased and acidic taxa declined, indicating that the lake was recovering (Fig. 2B).

The chrysophyte stratigraphy also records marked floristic shifts in *Mallomonas* and *Synura* species. The first shift started in the 1920s, when *S. petersenii* and the acidic and metal-tolerant *S. echinulata* started to increase and the pH generalist *M. crassisquama* started to decline. Since about 1960 the relative abundance of *M. crassisquama* started to increase and *S. petersenii* declined, but in the surface sediment, *S. petersenii* has modestly increased once again and *S. echinulata* has declined. In the 1980s, acidic taxa started to decline, ensuing an increase in other common taxa (Fig. 3B).

The diatom- and chrysophyte-inferred pH profiles indicate that the lake's preindustrial pH ranged between 5.8 and 6.1 (Fig. 4C). Acidification in George Lake started at about the 1920s and the inferred lake water pH reached its lowest value in the 1960s when diatom- and chrysophyte-inferred pH were close to 5.3. However, since about 1970, inferred lake water pH has started to recover, and the surface sediment diatom-inferred pH (5.6) and chrysophyte-inferred pH (5.4) are close to the measured pH value of 5.7 in 1987. Lake water pH measurements had an annual average pH of 5.2 in 1969 (Beamish 1974), a range of 4.8–5.3 during 1972 and 1973 (Beamish and Van Loon 1977), and an average of 5.5 reported for 1976, 1978, and 1979 (Bleiwas et al. 1984). The measured values are close to our diatom- and chrysophyte-inferred pH values (5.4 and 5.3, respectively) for that period. However, similar to Lumsden Lake, the 6.5 pH reading measured using colorimetric techniques in 1961 by the Ontario Department of Lands and Forests (cited in Beamish and Harvey 1972) is likely to be erroneous. Recent lake water pH measurements made by the Ontario Ministry of the Environment (W. Keller, unpubl. data) also indicate recent lake water pH recovery; for example, in 1981, 1983, 1985, 1987, and 1988, the measured pH values were 5.35, 5.34, 5.43, 5.73, and 5.69, respectively.

Although similar to Lumsden Lake, inferred [Ni] in George Lake commenced to increase in 1920. Inferred [Al] also started to increase about the same time in George Lake. This is most likely because acidification of this lake coincided with the period of increased Ni input in the 1920s whereas in Lumsden Lake, rapid acidification occurred almost 50 yr after the increase of [Ni] deposition. By the 1950s, the inferred Al and Ni values reached their maximum levels (Fig. 4D), but since then, inferred concentrations have stabilized and have also shown a modest, albeit statistically insignificant, recovery.

Although Lumsden and Acid lakes have lost their fish assemblages, George Lake maintains a viable fishery (Beamish and Harvey 1972); however, between 1965 and 1973 the number of fish species declined from 13 to 11 (Harvey 1975). The survival of fish in George Lake is most likely because this lake had not acidified (and [Al] did not increase) to the same extent as our other two study lakes.

Acid Lake

In comparison with the striking diatom shifts recorded during this century in Lumsden and George lakes, Acid Lake's diatom flora has only changed modestly in the past (Fig. 2C). With the exception of small shifts in *Eunotia* species, *M. distans*, and *A. ralfsii* v. *americana*, the percent abundance of the majority of diatom taxa remained relatively unchanged until about 1960. However, since then, many acid water taxa (e.g. *Eunotia* species, *M. distans, M. lirata, F. rhomboides* v. *saxonica*, and *F. magaliesmontana*) have increased in abundance. In the most recent sediment, more circumneutral and pH-indifferent taxa, such as *C. comta, C. stelligera, Anomoeoneis vitrea*, and *T. flocculosa* strain IIIp, have increased in abundance (Fig. 2C).

In contrast with the diatoms, chrysophyte changes have been more striking (Fig. 3C). The first shift started about 1930 when *M. hindonii* and *S. echinulata* started to increase in abundance whereas *Mallomonas pseudocoronata* and *M. punctifera* declined. *Mallomonas crassisquama* also started to decline about the same time, but its population had a small peak at around 1945. Since about 1980, more acidic indicator taxa (*S. echinulata* and *M. hindonii*) started to decline, with compensatory increases in *M. crassisquama* (Fig. 3C). This recent shift appears to be associated with the possible recovery in the lake; however, no recent recovery has occurred in circumneutral to alkaline taxa (e.g. *M. pseudocoronata* and *M. punctifera*), suggesting that the lake has not returned to its pre-1930 water chemistry.

The diatom- and chrysophyte-inferred pH profiles indicate that the lake's preindustrial pH ranged between 5.6 and 6.1 (Fig. 4E). Our diatom inference suggests only modest declines in lake water pH by 1960 whereas chrysophytes indicate a decline of about 0.5 of a pH unit. The pattern appears to be similar to the differences observed in Lumsden Lake, suggesting that chrysophytes are responding to spring pH depressions, whereas diatoms are inferring average lake water pH. The lake recorded its lowest inferred pH about 1980, when diatom- and chrysophyte-inferred pH values were 5.2 and 4.7, respectively (Fig. 4E). Towards the surface of the core, there appears to be some recovery; however, the trend is more pronounced for the chrysophyte-inferred pH. The surface sediment chrysophyte-inferred pH (4.9) is essentially identical to the 1987 measured pH of 4.92.

The diatom-inferred Al profile indicates that lake water [Al] started to increase about 1960 (Fig. 4F). The timing corresponds closely with the major increase of *M. hindonii* and the decline of *A. ralfsii* v. *americana* (Fig. 2C). *Mallomonas hindonii* is an indicator of acidic waters containing high [Al] whereas *A. ralfsii* v. *americana* is more competitive in acidic waters that have low [Al]. Parallel to the lake water pH recovery, inferred [Al] declined towards the surface of the core. For the surface sediment, the diatom-inferred [Al] is 140 μg/L whereas the 1987 measured [Al] is 250 μg/L (Fig. 4F; Table 1). As observed for Lumsden and George lakes, the increase of inferred [Ni] since about 1910 closely correlates with mining and smelting activity in Sudbury. The inferred [Ni] peaked in the 1920s and again in the 1950s, but thereafter, [Ni] has recovered to near preindustrial levels.

Until the mid-1960s, local fishermen recall a viable sport fishery in the lake. However, in 1968, the total catch was only one white sucker, six lake herring, and 25 lake chub (*Couesius plumbeus*) (Beamish and Harvey 1972). The sampling of Acid Lake in 1972 and 1973 yielded no fish at all (Harvey 1975). The timing of fish loss from Acid Lake closely corresponds with the increase in lake water [Al], although prior to 1960 the fish community was able to survive at an inferred pH range of 5.0–5.25.

General Discussion

In addition to SO_2 and metal inputs from the Sudbury smelters, the Killarney region also receives sulphate brought in by warm fronts carrying polluted air masses from southern Ontario and the eastern United States (Chan et al. 1982). The cause of acidification in our study lakes is clearly anthropogenic, as sulphate export from the sulfide-bearing strata in the Killarney region is minimal and the input of organic acidity to lakes from humic and fulvic acids is small (Glooschenko and Stevens 1986).

Although acidification and metal contamination of Killarney Park lakes have been known for some time, our study provides important information on the timing, extent, and rate of acidification of these lakes. Our study shows that during this century, acidification has occurred in the Killarney Provincial Park lakes; however, the timing and the magnitude of acidification have been different among lakes.

George Lake is poorly buffered (Gunn and Keller 1980) and drains an exposed rocky drainage basin with very little soil whereas the watersheds of Lumsden and Acid lakes have soil overburdens. This may be one possible reason why George Lake started to acidify in the 1920s, about the same time that stacks were installed at metallurgical installations in Sudbury. It is also possible that pockets of carbonate-containing rocks in the watersheds of Lumsden and Acid lakes provided some buffering and thus delayed the onset of rapid acidification until about 1960, when presumably the buffering was exhausted. Although it is difficult to identify why George Lake did not acidify to the level we observed in Lumsden and Acid lakes, hydrological differences may be important. It is also possible that the cultural activity in the lake's drainage basin since the mid-1960s has lessened the effect of acid precipitation. The inferred pH profiles indicate that since the early 1950s, lake water pH has stabilized in George Lake (Fig. 4C). Killarney Park was established in 1964 and currently there are 122 campsites and two beaches in George Lake's campground (OMNR 1986). There are no campgrounds on Lumsden and Acid lakes.

Although increases in lake water [Al] were probably due to increased mobility of Al as a result of acidification, the Ni inputs to the lakes were mainly atmospheric. As observed for Lumsden and Acid lakes, fish extirpation in Killarney Provincial Park lakes can be attributed to acidification and high lake water [Al]. Recent recovery coincides with reductions in SO_2 emissions from the Sudbury smelter since the early 1970s. Our study provides paleolimnological evidence that, in addition to chemical recovery (Keller et al. 1986), recent biological recovery has occurred in lakes located as far as 60 km from the Sudbury point sources.

Acknowledgements

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References

Asbury, C. E., F. A. Vertucci, M. D. Mattson, and G. E. Likens. 1989. Acidification of Adirondack lakes. Environ. Sci. Technol. 23: 362–365.

Baker, J. P., and C. L. Schofield. 1980. Aluminum toxicity to fish as related to acid precipitation and Adirondack surface water quality, p. 292–293. *In* D. Drabløs and A. Tollan [ed.] Ecological impact of acid precipitation. SNSF Project, Oslo, Norway.

Battarbee, R. W. 1973. A new method for the estimation of absolute microfossil numbers, with special reference to diatoms. Limnol. Oceanogr. 18: 647–653.

1986. Diatom analysis, p. 520–570. *In* B. E. Berglund [ed.] Handbook of Holocene palaeoecology and palaeohydrology. John Wiley and Sons, New York, NY.

Battarbee, R. W., J. Mason, I. Renberg, and J. F. Talling [ed.] 1990. Palaeolimnology and lake acidification. The Royal Society, London. 445p.

Beamish, R. J. 1974. Growth and survival of white suckers (*Catostomus commersoni*) in an acidified lake. J. Fish. Res. Board Can. 31: 49–54.

Beamish, J., and H. H. Harvey. 1972. Acidification of La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Beamish, R. J., and J. C. Van Loon. 1977. Precipitation loading of acid and heavy metals to a small acid lake near Sudbury, Ontario. J. Fish. Res. Board Can. 34: 649–658.

Binford, M. W. 1990. Calculation and uncertainty analysis of ^{210}Pb data for PIRLA project lake sediment cores. J. Paleolimnol. 3: 253–267.

Birks, H. J. B., S. Juggins, and J. M. Line. 1990a. Lake surface-water chemistry reconstructions from palaeolimnological data, p. 301–313. *In* J. J. Mason [ed.] The surface waters acidification programme. Cambridge University Press, Cambridge.

Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson, and C. J. F. ter Braak. 1990b. Diatoms and pH reconstructions. Philos. Trans. R. Soc. Lond. Ser. B 327: 263–278.

Bleiwas, A. S. H., P. M. Stokes, and M. M. Olaveson. 1984. Six years of plankton studies in the La Cloche region of Ontario, with special reference to acidification. Verh. Int. Ver. Limnol. 22: 332–337.

Chan, W. H., J. S. Tang, and M. A. Lusis. 1982. An analysis of the impact of the smelter emissions on precipitation quality and wet deposition in the Sudbury area: Sudbury environmental study event precipitation network results. Ont. Minist. Environ. Rep. SES 006/82: 72 p.

Charles, D. F., R. W. Battarbee, I. Renberg, H. van Dam, and J. P. Smol. 1989. Paleoecological analysis of diatoms and chrysophytes for reconstructing lake acidification trends in North America and Europe, p. 207–276. *In* S. A. Norton, S. E. Lindberg, and A. L. Page [ed.] Acid precipitation. Vol. 4, Soils, aquatic processes and lake acidification. Springer-Verlag, New York, NY.

Cumming, B. F., J. P. Smol, and H. J. B. Birks. 1992. Scaled chrysophytes (Chrysophyceae and Synurophyceae) from Adirondack drainage lakes and their relationship to measured environmental variables. J. Phycol. 28: 162–178.

Dickman, M., and S. S. Rao. 1989. Diatom stratigraphy in acid-stressed lakes in the Netherlands, Canada, and China, p. 115–143. *In* S. S. Rao [ed.] Acid stress and aquatic microbial interactions. CRC Press, Inc., Boca Raton, FL.

DILLON, P. J., R. A. REID, AND R. GIRARD. 1986. Changes in the chemistry of lakes near Sudbury, Ontario following reductions of SO_2 emissions. Water Air Soil Pollut. 31: 59–65.

DIXIT, A. S., S. S DIXIT, AND J. P. SMOL. 1992. Algal microfossils provide high temporal resolution of environmental change. Water Air Soil Pollut. 62: 75–87.

DIXIT, S. S., A. S. DIXIT, AND J. P. SMOL. 1989a. Lake acidification recovery can be monitored using chrysophycean microfossils. Can. J. Fish. Aquat. Sci. 46: 1309–1312.

1989b. Relationship between chrysophyte assemblages and environmental variables in seventy-two Sudbury lakes as examined by canonical correspondence analysis (CCA). Can. J. Fish. Aquat. Sci. 46: 1667–1676.

1991. Multivariable environmental inferences based on diatom assemblages from Sudbury (Canada) lakes. Freshwater Biol. 26: 251–266.

GENSEMER, R. W. 1990. Role of aluminum and growth rate on changes in cell size and silica content of silica-limited populations of *Asterionella ralfsii* v. *americana* (Bacillariophyceae). J. Phycol. 26: 250–258.

GLEW, J. R. 1988. A portable extruding device for close interval sectioning of unconsolidated core samples. J. Paleolimnol. 1: 235–239.

GLOOSCHENKO, V., AND W. STEVENS. 1986. Sources of acidity in wetlands near Sudbury, Ontario. Sci. Total Environ. 54: 53–59.

GORHAM, E., AND A. G. GORDON. 1960. Some effects of smelter pollution northeast of Falconbridge, Ontario. Can. J. Bot. 38: 307–312.

GUNN, J. M., AND W. KELLER. 1980. Enhancement of the survival of rainbow trout (*Salmo gairdneri*) egg and fry in an acid lake through incubation in limestone. Can. J. Fish. Aquat. Sci. 37: 1522–1530.

1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

HARVEY, H. H. 1975. Fish populations in a large group of acid-stressed lakes. Verh. Int. Ver. Limnol. 19: 2406–2417.

HULSMAN, P. F., P. M. POWLES, AND J. M. GUNN. 1983. Mortality of walleye eggs and rainbow trout yolk-sac larvae in low-pH waters of the La Cloche Mountain area, Ontario. Trans. Am. Fish. Soc. 112: 680–688.

HUTCHINSON, T. C., AND M. HAVAS. 1986. Recovery of previously acidified lakes near Coniston, Canada following reductions in atmospheric sulphur and metal emissions. Water Air Soil Pollut. 28: 319–333.

KELLER, W., J. R. PITBALDO, AND N. I. CONROY. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. Water Air Soil Pollut. 31: 774–775.

LINE, J. M., AND H. J. B. BIRKS. 1990. WACALIB version 1.2 — a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging. J. Paleolimnol. 3: 170–173.

MUNIZ, I. P., AND H. LEIVESTAD. 1980. Toxic effects of aluminum on the brown trout, *Salmo trutta*, p. 84–92. *In* D. Drabløs and A. Tollan [ed.] Ecological impact of acid precipitation. SNSF Project, Oslo, Norway.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1986. Killarney Provincial Park. Map, Queen's Printer for Ontario, Ontario.

PILLSBURY, R. W., AND J. C. KINGSTON. 1990. The pH independent effects of aluminum on cultures of phytoplankton from an acidic Wisconsin lake. Hydrobiologia 194: 225–233.

SMOL, J. P. 1986. Chrysophycean microfossils as indicators of lakewater pH, p. 275–287. *In* J. P. Smol, R. W. Battarbee, R. B. Davis and J. Meriläinen [ed.] Diatoms and lake acidity. Dr. W. Junk, Dordecht, The Netherlands.

STEVENSON, A. C., H. J. B. BIRKS, R. J. FLOWER, AND R. W. BATTARBEE. 1989. Diatom-based pH reconstruction of lake acidification using canonical correspondence analysis. Ambio 18: 228–233.

STOKES, P. M., AND Y. K. YUNG. 1986. Phytoplankton in selected LaCloche (Ontario) lakes, pH 4.2–7.0, with special reference to algae as indicators of chemical characteristics, p. 57–72. *In* J. P. Smol, R. W. Battarbee, R. B. Davis and J. Meriläinen [ed.] Diatoms and lake acidity. Dr. W. Junk, Dordecht, The Netherlands.

TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 1966: 1167–1179.

TER BRAAK, C. J. F., AND H. VAN DAM. 1989. Inferring pH from diatom: a comparison of old and new calibration methods. Hydrobiologia 178: 209–223.

Chemical Responses of Acidic Lakes in the Sudbury, Ontario, Area to Reduced Smelter Emissions, 1981–89

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Monitoring of acidic lakes in the Sudbury, Ontario, area showed that general changes in water quality (increases in pH and acid-neutralizing capacity; decreases in concentrations of SO_4^{2-}, Ca^{2+}, Mg^{2+}, Al, and Mn) have continued through the mid-1980's, following substantial reductions in sulphur emissions from area smelters in the late 1970's. By the late 1980's, these trends had levelled off, or even reversed in some lakes. No general, temporal trends were evident during the 1980's for concentrations of Cu, Ni, or Zn, metals directly associated with the smelter emissions. The widespread water quality improvements seen in lakes of the Sudbury area provide very strong support for the use of source controls to combat aquatic acidification. However, the fact that many Sudbury area lakes are still highly acidic and metal contaminated demonstrates that additional emission controls, which are being implemented, are essential in this region.

La surveillance des lacs acides dans la région de Sudbury (Ontario) a montré que les changements généraux sur le plan de la qualité de l'eau (augmentation du pH et du potentiel de neutralisation de l'acide; diminution des concentrations de SO_4^{-2}, Ca^{+2}, Mg^{+2}, Al et Mn) ont continué dans le milieu des années 1980, après des réductions substantielles des émissions de soufre par les fonderies de la région à la fin des années 1970. À la fin des années 1980, ces tendances se sont stabilisées et se sont même renversées dans certains lacs. On n'a pu dégager aucune tendance temporelle générale durant les années 1980 sur le plan des concentrations de Cu, de Ni ou de Zn, métaux qui sont directement associés aux émissions des fonderies. Les améliorations généralisées de la qualité de l'eau observées dans les lacs de la région de Sudbury sont des arguments convaincants en faveur du recours à la réduction à la source pour lutter contre l'acidification aquatique. Toutefois, le fait que bon nombre de lacs de la région de Sudbury soient encore hautement acides et contaminés par les métaux démontre que les mesures additionnelles de réduction des émissions qui sont actuellement mises en oeuvre sont essentielles dans cette région.

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Lakes in northeastern Ontario have long been subjected to S and trace metal deposition associated with emissions to the atmosphere from the Sudbury metal smelting industry OCTF 1982; Nriagu 1984). Total sulphur deposition in the Sudbury area has not been well quantified; however, sulphur deposition rates are considered to be the highest in Ontario (>1.25 g·m^{-2}·yr^{-1}; Neary and Dillon 1988). Adverse effects on water quality resulting from the Sudbury emissions have been recognized for decades (Gorham and Gordon 1960) and have been shown to influence a very large geographical area (Beamish and Harvey 1972; Conroy et al. 1976; Keller et al. 1980; Pitblado et al. 1980; Neary et al. 1990). Within this zone of effect, high acidity and elevated concentrations of trace metals have had very severe effects on aquatic biota (Beamish and Harvey 1972; Sprules 1975; Keller and Pitblado 1984; Yan and Miller 1984; Beggs and Gunn 1986; MacIsaac et al. 1987; and others).

The situation in Sudbury, however, has not been static. Large reductions in sulphur emissions (Fig. 1) and associated emissions of trace metals have occurred over the years, and water quality improvements have been observed in many area lakes, based on comparisons of survey data from the mid-1970's and early 1980's (Keller and Pitblado 1986). Other studies have also shown chemical improvements in area lakes related to reduced smelter emissions (LaZerte and Dillon 1984; Dillon et al. 1986; Hutchinson and Havas 1986; Gunn and Keller 1990), and evidence of biological improvements is mounting (MacIsaac et al. 1986; Gunn and Keller 1990; Keller and Yan 1991).

Since 1981, annual monitoring has been conducted on a set of 41 acidic Sudbury area lakes (Fig. 2) in order to permit assessment of general long-term trends in water quality resulting from emission reductions. These lakes, here termed the Extensive Survey Lakes, vary in morphometry, trophic status, and distance from Sudbury (Table 1). All the lakes were acidified (pH ≤ 5.8) at the beginning of this study. In addition, data are available from Swan Lake, a small (5.8 ha), shallow ($Z_{max} = 8.8$ m), acidic lake close (13 km) to Sudbury that has been intensively sampled every year since 1982. The chemical

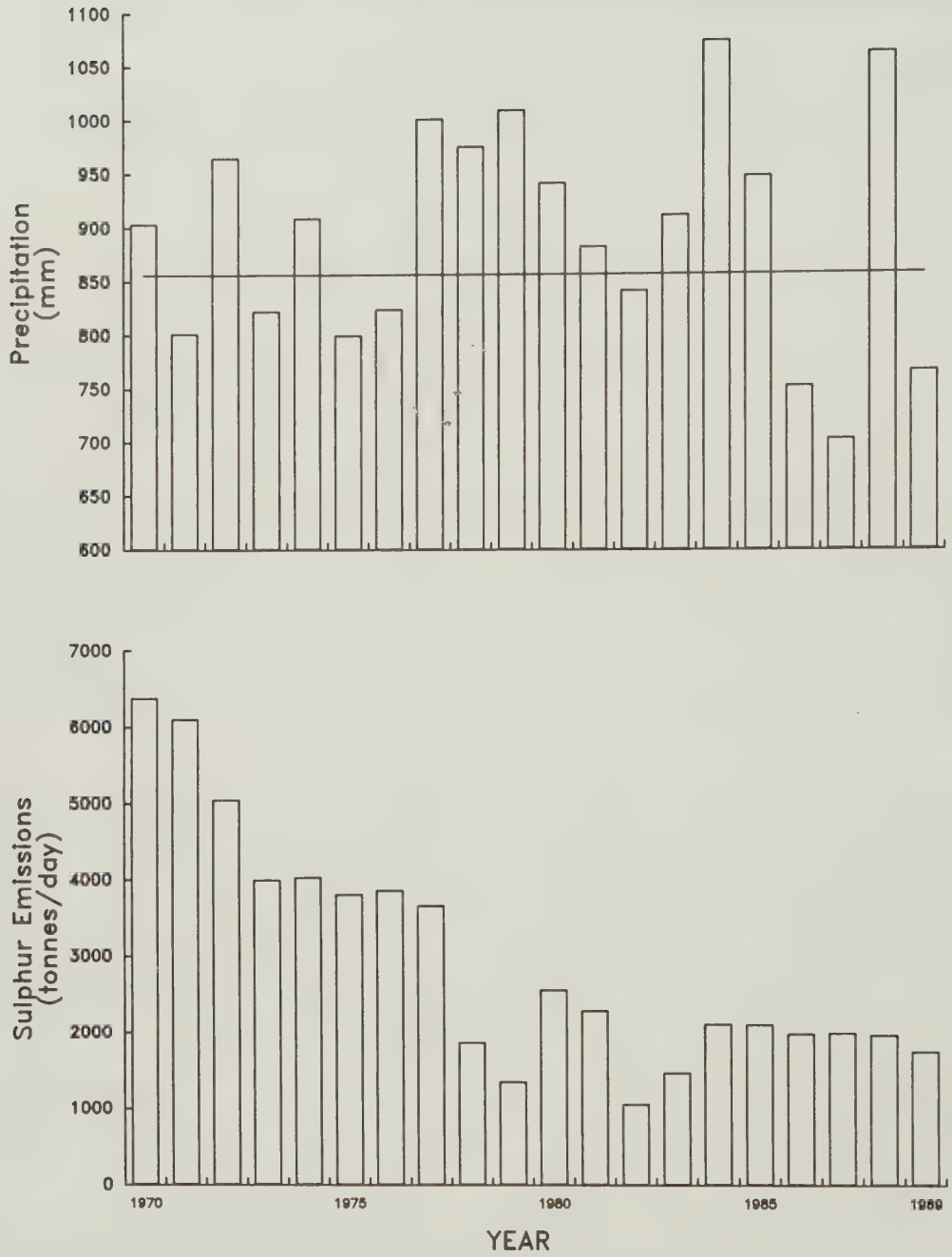

FIG. 1. Patterns in average daily SO_2 emissions and total annual precipitation (long-term average precipitation is indicated by the horizontal line) in the Sudbury area, 1970–89. Combined SO_2 emissions for Inco Limited and Falconbridge Nickel Mines Limited are given. Precipitation data are for the Sudbury Airport, provided by Environment Canada.

recovery of Swan Lake up to 1984 has previously been reported (Dillon et al. 1986; MacIsaac et al. 1986).

In this paper, we examine these data sets to investigate patterns of chemical recovery. Despite evidence of generally reduced sulphur deposition in North America (Hedin et al. 1987; Dillon et al. 1988), outside the Sudbury area, evidence for lake recovery is very rare (Kelso and Jeffries 1988). Such assessment of lake recovery after emission reductions is, however, essential to evaluate the effectiveness of emission abatement as a solution to the acid deposition problem.

Methods

The 41 Extensive Survey Lakes were sampled once annually, during summer stratification, over the period 1981–89. Water samples were collected from a central location on each lake as non-volume-weighted Tygon tube composites through the epilimnion and metalimnion (MOE 1979). In Swan Lake, whole lake water samples were collected from a central station on a twice-monthly basis during the ice-free seasons of 1982–89. Aliquots from discrete depth samples were combined in pro-

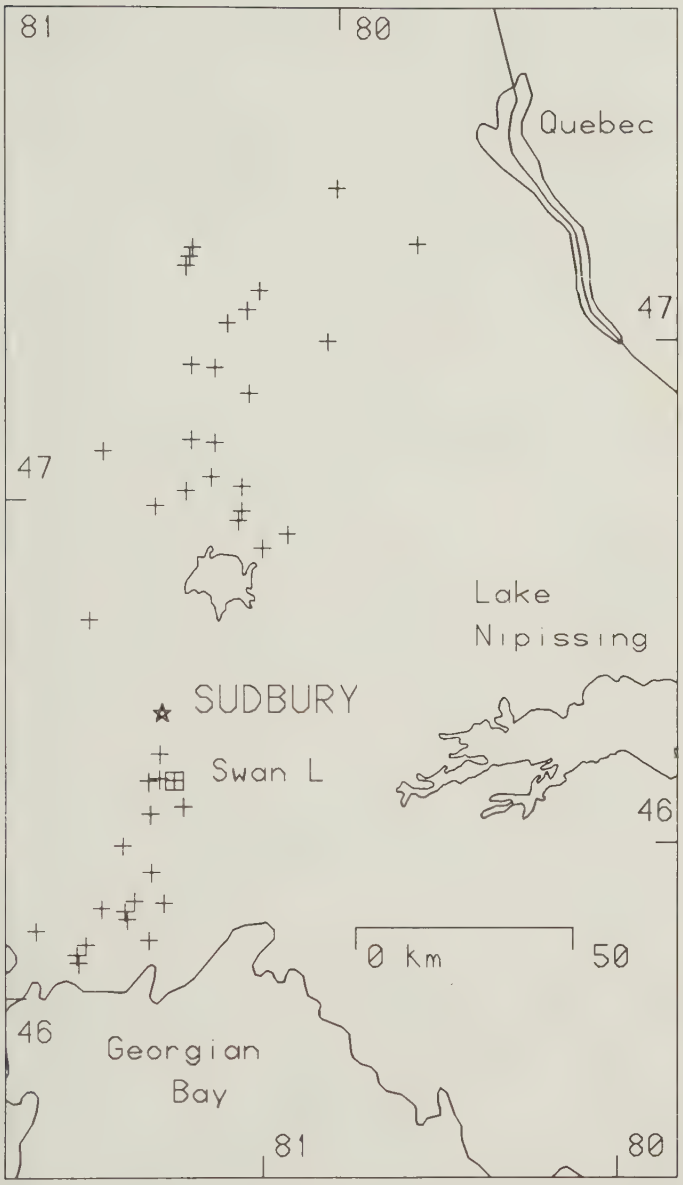

FIG. 2. Locations of the Extensive Survey Lakes (+) and Swan Lake (□).

TABLE 1. General chemical and physical characteristics of the Extensive Survey Lakes. Chemistry data are based on sampling in 1981.

	Mean	Range
Distance from Sudbury (km)	62	10–128
Lake area (ha)	280	14.7–1511
Maximum depth (m)[a]	31.0	9.4–90.3
Total P (μg/L)	5	1–14
Dissolved organic carbon (mg/L)	1.8	0.0–6.6
Secchi transparency (m)	9.9	2.1–23.4
Conductivity (μS/cm)	41	31–73

[a]Only available for 35 lakes.

portion to lake morphometry to yield a volume-weighted sample.

Analytical methods followed MOE (1981). Acid-neutralizing capacity (ANC) and pH were measured in the Sudbury Ministry of the Environment (MOE) Laboratory. Other analyses were conducted at the Toronto MOE laboratory.

Results

Extensive Survey Lakes

In 1981, at the beginning of this study, the pH of the study lakes ranged from 4.3 to 5.8, and many lakes exhibited elevated concentrations of trace metals (Cu, 1–94 μg/L; Ni, 2–340 μg/L; Zn, 3–31 μg/L; Al, 20–840 μg/L; Mn, 52–278 μg/L). Of these metals, concentrations of Cu and Ni in lake waters were clearly related to distance from Sudbury; concentrations of Zn showed highest concentrations near Sudbury, although patterns related to distance were not as clear; and concentrations of Al and Mn did not show any apparent relationship to distance from the Sudbury smelters (Fig. 3). Concentrations of SO_4^{2-}, Ca^{2+}, and Mg^{2+} were related to distance from Sudbury, while no clear relationship with distance was evident for pH and ANC (Fig. 3). Concentrations of parameters that did show clear relationships to distance were most conspicuously elevated within about 30 km of Sudbury (Fig. 3).

Over the entire study period, 1981–89, the dominant pattern in water chemistry was a trend toward decreased acidity, lower concentrations of SO_4^{2-}, Ca^{2+}, and Mg^{2+}, and reduced concentrations of Al and Mn (Fig. 4). Overall, comparing 1981 and 1989, increases in pH and ANC were observed in 95 and 97% of the lakes, respectively, and decreases in SO_4^{2-}, Ca^{2+}, and Mg^{2+} were observed in 82, 84, and 81% of the lakes, respectively (Table 2). Concentrations of Al and Mn also showed general trends of reductions over time (Fig. 4), with overall decreases in 59 and 77% of the lakes, respectively (Table 2). No clear patterns of change were observed for other trace metals.

Examination of annual variations (Fig. 4), however, indicates that changes in water quality were not constant through the study period. The general pattern observed was one of consistent annual improvement through to the mid-1980's, followed by slightly increased concentrations of SO_4^{2-}, Al, and Mn and decreased pH and ANC in the late 1980's (Fig. 4; Table 2). In the last study year (1989), the pH of the lakes ranged from 4.4 to 6.0.

Swan Lake

Temporal chemistry patterns in Swan Lake showed general agreement with results from the Extensive Survey Lakes. Trends were observed of increasing pH and ANC and decreasing concentrations of SO_4^{2-}, Ca^{2+}, Mg^{2+}, Al, and Mn between 1982 and 1987, followed by an abrupt reversal of this pattern in 1988 (Fig. 5). Concentrations of Cu, Ni, and Zn also showed substantial increases in 1988. Detailed examination of the data indicated that the decline in water quality actually commenced in the fall of 1987, with the onset of autumn rains and runoff. However, dramatic changes in chemistry were evident after spring runoff in 1988. Temporal chemistry trends in Swan Lake were very pronounced. For example, between 1982 and 1987, mean ice-free period pH increased from 4.8 to 5.4, only to decline to 4.5 in 1988 (Fig. 5).

Discussion

Monitoring of lakes in the Sudbury area has demonstrated that major reductions of sulphur and trace metal emissions to the atmosphere in the 1970's have lead to rapid increases in pH and decreases in the concentrations of SO_4^{2-}, Cu, and Ni in some area lakes (Dillon et al. 1986; Hutchinson and Havas 1986; Keller and Pitblado 1986). The present study examines

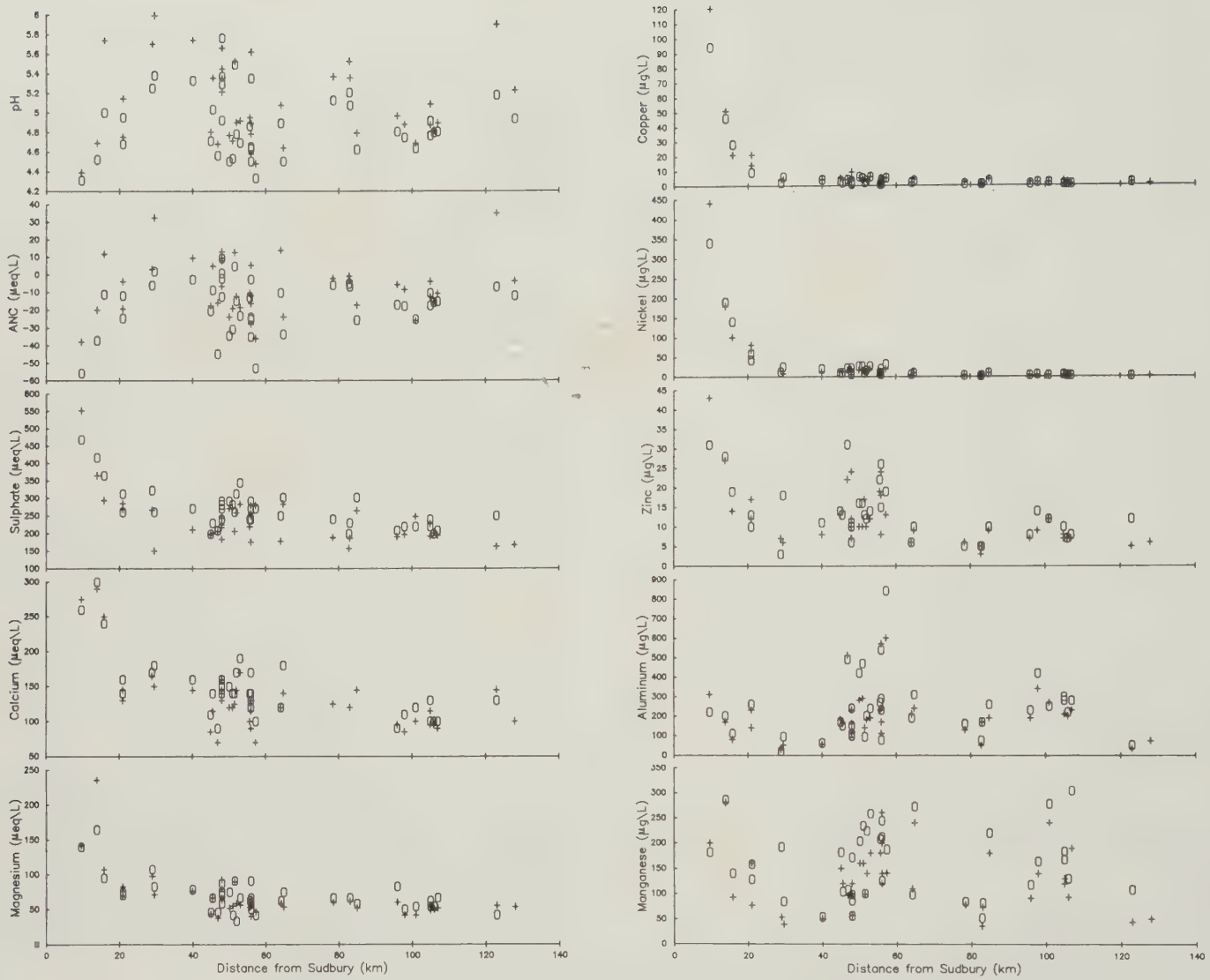

FIG. 3. Relationships of chemistry variables with distance in 1981 (○) and 1989 (+) for the Extensive Survey Lakes.

long-term trends in these and other key parameters, including Al, Mn, ANC, and base cation concentrations and indicates that a clear, very widespread pattern of recovery has continued well into the 1980's. General increases in pH and ANC and decreases in concentrations of SO_4^{2-}, Ca^{2+}, Mg^{2+}, Al, and Mn occurred between 1981 and 1987.

Because during the overall period examined here (1981–89), emissions of sulphur from the Sudbury smelters were relatively uniform (Fig. 1), this pattern likely reflects the continuing influence of previous large-scale emission reductions (Fig. 1 and OCTF 1982) as modified by lake response time and perhaps augmented by the effect of two years (1982 and 1983) of comparatively lower SO_2 emissions (Fig. 1). Given that the average hydraulic retention time of the Extensive Survey Lakes is about 3 yr, the full effect of a change in input to these lakes would be expected to take close to a decade to be fully realized. Thus, a levelling off of changes in the mid-1980's that were precipitated by emission reductions in the late 1970's is consistent with general expectations based on hydrological considerations.

During the latter years of this study, the observed trends of chemical recovery did not continue and, in fact, often showed a reversal. Between 1987 and 1989, the dominant trends observed in the study lakes were decreases in pH and ANC and increases in concentrations of SO_4^{2-}, Al, and Mn (Fig. 4; Table 2). While this pattern may still partially reflect "lag time" from previous short-term changes in emissions (i.e. comparatively low emissions in 1982 and 1983, increasing to higher relatively static levels over the period 1984–89; Fig. 1), examination of precipitation data (Fig. 1) indicates that extreme variations in the amount of precipitation received over the study period can largely explain the observed declines in water quality.

The probable explanation is that extensive storage and oxidation of sulphur occurred in lake watersheds during the extremely dry years of 1986 and 1987. These were the two driest years recorded during the two-decade period beginning in 1970 (Fig. 1). Dry deposition of sulphur in the Sudbury area is poorly quantified, but is known to be substantial. Dillon (1984) and Jeffries (1984) demonstrated that dry deposition was a dominant component of sulphur inputs to lakes near Sudbury. Since dry deposition near the smelter is a relatively inefficient removal mechanism (Chan et al. 1984), dry deposition of sulphur is undoubtedly an input of general importance to lakes in the Sudbury region.

With the return of abundant precipitation in 1988 (Fig. 1), there was apparently a very large export of acid and sulphur

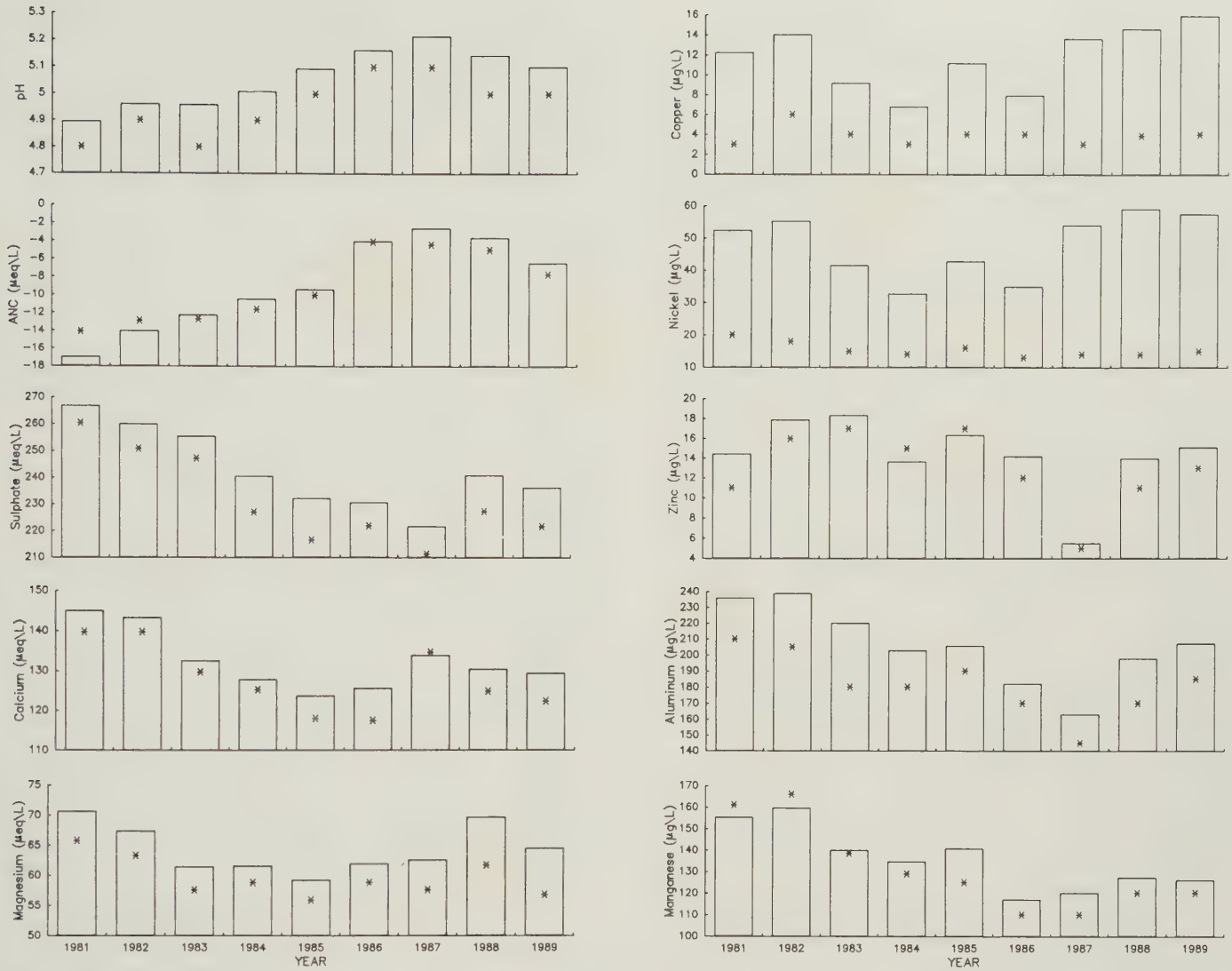

FIG. 4. Mean (top of bar) and median (asterisk) values by year (1981–89) for chemical characteristics of the Extensive Survey Lakes (*n* for each parameter is given in Table 2).

TABLE 2. Percentages of the Extensive Survey Lakes that showed increases (+), decreases (−), or no change (0) between specific study years.

		Study period								
		1981 vs. 1989			1981 vs. 1987			1987 vs. 1989		
Parameter	n[a]	+	0	−	+	0	−	+	0	−
pH	38	95	0	5	100	0	0	18	0	82
ANC	38	97	0	3	100	0	0	11	0	89
Ca^{2+}	26	8	8	84	8	23	69	19	12	69
Mg^{2+}	26	15	4	81	8	4	88	46	23	31
SO_4^{2-}	34	18	0	82	3	0	97	68	6	26
Al	34	35	6	59	12	0	88	79	15	6
Mn	34	23	0	77	6	0	94	47	21	32
Cu[b]	13	70	15	15	54	23	23	69	31	0
Ni[b]	13	54	7	39	54	0	46	77	8	15
Zn[b]	13	54	0	46	0	0	100	84	8	8

[a]Only includes lakes with a complete record of each parameter across the study years; thus, *n* varies.
[b]Only includes lakes within 50 km of Sudbury.

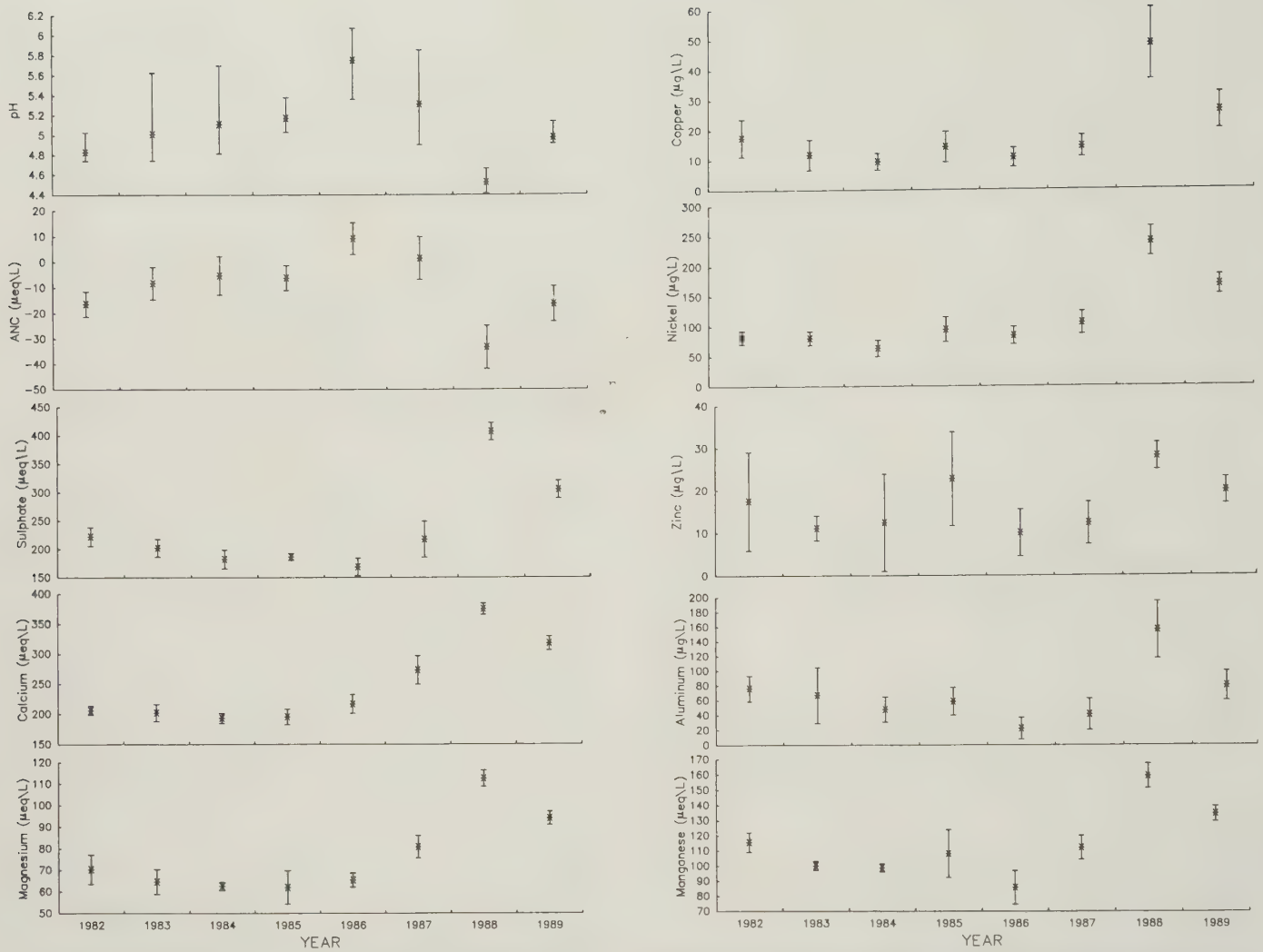

FIG. 5. Temporal chemistry trends (annual $\bar{x} \pm$ SD) in Swan Lake, 1982–89 (n ranged from 11 to 13 samples per year). For pH, the range in individual values is given.

stored in lake catchments during dry conditions (Fig. 4 and 5). In the extensively studied Swan Lake, temporal patterns suggest that water quality declines actually commenced after fall runoff in 1987 but that major changes followed spring runoff in 1988 (Fig. 5). This mechanism would also be expected to liberate quantities of Ca^{2+}, Mg^{2+}, Al, and Mn. Mineral weathering is driven by strong anthropogenic acids in the Sudbury area (Jeffries et al. 1984). As well, wetlands, a ubiquitous component of northeastern Ontario watersheds, may be important in storing sulphur (Bayley et al. 1986; Wood 1989; Dillon and LaZerte 1992) and may release cations as well as sulphur during wet periods. Thus, the above scenario based on precipitation patterns is consistent with the general trends observed in lake water chemistry in the latter years of this study.

Changes in lake water levels may also in some cases have contributed to the chemistry changes observed between 1987 and 1988. As a result of extremely dry conditions, lake levels were very low by 1987, and in some lakes such as Swan, observations showed that substantial areas of littoral sediments were exposed (W. Keller, pers. obs.). Because littoral sediments may be anoxic below the surface (Cook et al. 1986), exposure to the air would probably lead to substantial oxidation. Upon resubmergence, especially with acidic runoff water, mobilization of sulphur, base cations, and metals to the water column would be expected. Increases in acidity and concentrations of metals and base cations resulting from draining and reflooding have been observed in Laurentian Lake, near Sudbury (Keller 1984).

It is noteworthy that an extreme reversal of water quality conditions occurred in Swan Lake which is very close to the smelters and has a rapid flushing time (<1 yr). This suggests that small, hydrologically responsive lakes may be subjected to substantial fluctuations in chemistry related to precipitation patterns, and thus the effects of acid deposition may be amplified in such lakes. In general agreement with the findings of Schindler et al. (1990), the observations on temporal chemical patterns in Swan Lake and the Extensive Survey Lakes point out the importance of considering climatic factors in the interpretation of long-term data sets. While our results deal with drainage-dominated lakes, Webster et al. (1990) have suggested that climatic variations can also have substantial influences on the acid–base status of seepage-type lakes.

Despite the overall substantial improvements that have occurred in the Sudbury area over the years, it is also apparent that many area lakes continue to exhibit severe water quality impairment. All but one of the present study lakes currently (1989) had pH < 6.0, a level below which significant biological damage is expected to occur (Schindler 1988; Baker et al.

1990; Keller et al. 1990; Matuszek et al. 1990; RMCC 1990), and 17, 12, and 2% of the lakes, respectively, had Cu, Ni, and Zn concentrations exceeding guidelines for the protection of fish and aquatic life (MOE 1984). Substantially elevated concentrations of Cu and Ni were essentially restricted to lakes very close (<30 km) to Sudbury (Fig. 3).

Substantial decreases in trace metal emissions occurred in the late 1970's, and corresponding decreases in trace metal concentrations were observed between the mid-1970's and early 1980's in area lakes (Keller and Pitblado 1986). Monitoring from 1981 to 1989, however, has not shown any clear trend toward continuing decreases in Cu, Ni, or Zn, metals directly related to the smelter emissions (Fig. 4 and 5). It appears that substantial further reductions in metal deposition would be required to rehabilitate heavily impacted lakes close to the Sudbury smelters. Previous observations (Hutchinson and Havas 1986; Keller and Pitblado 1986) suggest that further trace metal emission reductions will lead to decreases in lake water concentrations of metals. As well, it is important to note that the general patterns of chemical recovery in Sudbury area lakes appear to have stopped by the late 1980's. The need for additional abatement measures, such as those initiated by MOE (1987) to achieve future sulphur emission reductions, is clear.

The Sudbury area has provided a unique opportunity for large-scale assessment of the effects of major reductions in acid-forming emissions on lake water quality. The empirical results presented here agree well with experimental results from a Norwegian catchment showing increased ANC and reductions in concentrations of SO_4^{2-} and base cations in runoff, after exclusion of acid deposition (Wright et al. 1988). Our documentation of widespread increases in pH and ANC accompanied by decreases in concentrations of SO_4^{2-}, base cations, Al, and Mn following reductions in acidic deposition provides very strong support for source control strategies to address the lake acidification problem in the Sudbury area and elsewhere.

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References

Baker, J. P., D. P. Bernard, S. W. Christensen, and M. J. Sale. 1990. Biological effects of changes in surface water acid-base chemistry. State of Science/Technology Rep. 13. National Acid Precipitation Assessment Program, Washington DC.

Bayley, S. E., R. S. Behr, and C. A. Kelly. 1986. Retention and release of S from a freshwater wetland. Water Air Soil Pollut. 31: 101–114.

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Beggs, G. L., and J. M. Gunn. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711–717.

Chan, W. H., R. J. Vet, Chul-Un Ro, A. J. S. Tang, and M. A. Lusis. 1984. Impact of Inco smelter emissions on wet and dry deposition in the Sudbury area. Atmos. Environ. 18: 1001–1008.

Conroy, N. I., K. Hawley, W. Keller, and C. Lafrance. 1976. Influences of the atmosphere on lakes in the Sudbury area. Proc. First Spec. Symp. Atmos. Contrib. Chem. Lake Waters. J. Int. Assoc. Great Lakes Res. 2: 146–165.

Cook, R. B., C. A. Kelly, D. W. Schindler, and M. A. Turner. 1986. Mechanisms of hydrogen ion neutralization in an experimentally acidified lake. Limnol. Oceanogr. 31: 134–148.

Dillon, P. J. 1984. The use of mass balances and mass balance models for the quantification of the effects of anthropogenic activities on lakes near Sudbury, Ontario, p. 284–347. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley & Sons, Inc., New York, NY.

Dillon, P. J., and B. D. LaZerte. 1992. Response of the Plastic Lake catchment, Ontario to reduced sulphur deposition Environ. Pollut. 77: 211–218.

Dillon, P. J., M. Lusis, R. A. Reid, and D. Yap. 1988. Ten-year trends in sulphate, nitrate and hydrogen deposition in central Ontario. Atmos. Environ. 22: 901–905.

Dillon, P. J., R. A. Reid, and R. Girard. 1986. Changes in the chemistry of lakes near Sudbury, Ontario following reductions of SO_2 emissions. Water Air Soil Pollut. 31: 59–66.

Gorham, E., and A. G. Gordon. 1960. The influence of smelter fumes upon the chemical composition of lake waters near Sudbury, Ontario, and upon the surrounding vegetation. Can. J. Bot. 30: 477–487.

Gunn, J. M., and W. Keller. 1990. Biological recovery of an acid lake following reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

Hedin, L. O., G. E. Likens, and F. H. Borman. 1987. Decrease in precipitation acidity resulting from decreased SO_4^{2-} concentration. Nature (Lond.) 325: 244–246.

Hutchinson, T. C., and M. Havas. 1986. Recovery of previously acidified lakes near Coniston, Canada following reductions in atmospheric sulphur and metal emissions. Water Air Soil Pollut. 29: 319–333.

Jeffries, D. S. 1984. Atmospheric deposition of pollutants in the Sudbury area, p. 118–154. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley & Sons, Inc., New York, NY.

Jeffries, D. S., W. A. Scheider, and W. R. Snyder. 1984. Geochemical interactions of watersheds with precipitation in areas affected by smelter emissions near Sudbury, Ontario, p. 196–241. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley & Sons, Inc., New York, NY.

Keller, N. 1984. Changes in the chemical composition of water, sediment, and aquatic plants related to the reflooding of a drained lake. Thesis, Laurentian University, Sudbury, Ont.

Keller, W., J. Gunn, and N. Conroy. 1980. Acidification impacts on lakes in the Sudbury, Ontario, Canada area, p. 228–229. *In* D. Drabløs and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., SNSF Project, Oslo, Norway.

Keller, W., and J. R. Pitblado. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acid deposition. Water Air Soil Pollut. 28: 283–292.

1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water Air Soil Pollut. 29: 285–296.

Keller, W., and N. D. Yan. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

Keller, W., N. D. Yan, K. Holtze, and J. R. Pitblado. 1990. Inferred effects of lake acidification on *Daphnia galeata mendotae*. Environ. Sci. Technol. 24: 1259–1261.

Kelso, J. R. M., and D. S. Jeffries. 1988. Response of headwater lakes to varying atmospheric deposition in north central Ontario, 1979–85. Can. J. Fish. Aquat. Sci. 45: 1905–1911.

LaZerte, B. D., and P. J Dillon. 1984. Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario. Can. J. Fish. Aquat. Sci. 41: 1664–1677.

MacIsaac, H. J., T. C. Hutchinson, and W. Keller. 1987. An analysis of planktonic rotifer assemblages from Sudbury, Ontario lakes of varying chemical composition. Can. J. Fish. Aquat. Sci. 44: 1692–1701.

MacIsaac, H. J., W. Keller, T. C. Hutchinson, and N. D. Yan. 1986. Natural changes in the planktonic Rotifera of a small acid lake near Sudbury, Ontario following water quality improvements. Water Air Soil Pollut. 31: 791–797.

Matuszek, J. E., J. Goodier, and D. L. Wales. 1990. The occurrence of cyprinids and other small fish species in relation to pH in Ontario lakes. Trans. Am. Fish. Soc. 119: 850–861.

MOE (Ontario Ministry of the Environment). 1979. Determination of the susceptibility to acidification of poorly buffered surface waters. Ont. Minist. Environ. Rep., Toronto, Ont. 21 p.

1981. Outlines of analytical methods. Ont. Minist. Environ. Rep., Toronto, Ont. 246 p. plus appendix.

1984. Water management — goals, policies, objectives and implementation procedures of the Ministry of the Environment. Ont. Minist. Environ. Rep., Toronto, Ont. 70 p.

1987. Countdown Acid Rain, summary and analysis of the second progress reports by Ontario's four major sources of sulphur dioxide. Ont. Minist. Environ. Rep., Toronto, Ont. 17 p.

Neary, B. P., and P. J. Dillon. 1988. Effects of sulphur deposition on lakewater chemistry in Ontario, Canada. Nature (Lond.) 333: 340–343.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ont. Minist. Environ. Rep., Toronto, Ont. 171 p.

NRIAGU, J. [ED.] 1984. Environmental impacts of smelters. John Wiley & Sons Inc., New York, NY.

OCTF (ONTARIO/CANADA TASK FORCE). 1982. Report of the Ontario/Canada Task Force for the development and evaluation of air pollution abatement options for Inco Limited and Falconbridge Nickel Mines Limited in the Regional Municipality of Sudbury, Ontario. Intergovernmental Task Force Report, Toronto, Ont. 255 p.

PITBLADO, J. R., W. KELLER, AND N. I. CONROY. 1980. A classification and description of some Northeastern Ontario lakes influenced by acid precipitation. J. Great Lakes Res. 6: 247–257.

RMCC (FEDERAL–PROVINCIAL RESEARCH AND MONITORING COORDINATING COMMITTEE). 1990. The 1990 Canadian long range transport of air pollutants and acid deposition report. Part 4: aquatic effects.

SCHINDLER, D. W. 1988. Effects of acid rain on freshwater ecosystems. Science (Wash., DC) 239: 149–157.

SCHINDLER, D. W., K. G. BEATY, E. J. FEE, D. R. CRUIKSHANK, E. R. DE BRUYN, D. L. FINDLAY, G. A. LINSEY, J. A. SHEARER, M. P. STAINTON, AND M. A. TURNER. 1990. Effects of climatic warming on lakes of the central boreal forest. Science (Wash., DC) 250: 967–970.

SPRULES, W. G. 1975. Midsummer crustacean zooplankton communities in acid stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

WEBSTER, K. E., A. D. NEWELL, L. A. BAKER, AND P. L. BREZONIK. 1990. Climatically induced rapid acidification of a soft water seepage lake. Nature (Lond.) 347: 374–376.

WOOD, J. A. 1989. Peatland acidity budgets and the effects of acid deposition. Discussion Paper No. 5. Ecol. Appl. Res. Div., Environment Canada, Ottawa, Ont. 34 p.

WRIGHT, R. F., E. LOTSE, AND A. SEMB. 1988. Reversibility of acidification shown by whole-catchment experiments. Nature (Lond.) 334: 670–675.

YAN, N. D., AND G. E. MILLER. 1984. Effects of deposition of acids and metals on chemistry and biology of lakes near Sudbury, Ontario, p. 244–282. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley & Sons, Inc., New York, NY.

Landsat Views of Sudbury (Canada) Area Acidic and Nonacidic Lakes

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Multivariate statistical procedures are used to establish empirical associations between acidity, visual lake water colour, dissolved organic carbon (DOC) concentrations, and Landsat-5 Thematic Mapper (TM) radiance data. Acidic lakes in an area northeast of Sudbury (Canada) are characterized by their clear, blue colours and very low DOC. With a subjective, three-class water colour grouping, 92% of the study lakes were correctly classified using TM data. Further, it is shown that DOC, the major component of water colour in this area, can be predicted within 1 mg/L of observed concentrations using TM data (multiple $r = 0.93$, $P < 0.01$). By deriving interrelationships between pH levels, water colour, and DOC, Landsat data provide a means to discriminate and map the acidic and nonacidic lakes of the study area. Examination of the reflectance characteristics of a single acidic lake (Bowland Lake) that has undergone neutralization suggests that Landsat data may be used to detect optical changes over time. However, the capability for monitoring the temporal dimension of lake acidification using satellite data has yet to be established.

Des méthodes d'analyse statistique multivariée sont utilisées pour établir des associations empiriques entre l'acidité, la couleur visuelle de l'eau du lac, les concentrations de carbone organique dissous (COD) et les données de radiance de l'appareil de cartographie thématique (TM) de Landsat-5. Les lacs acides de la région du nord-est de Sudbury (Canada) sont caractérisés par leur couleur bleue transparente et par de très faibles concentrations de COD. Avec un groupement subjectif de la couleur de l'eau selon trois classes 92 % des lacs étudiés ont été classés dans la bonne catégorie à partir des données du TM. En outre, nous montrons qu'il est possible de prédire la concentration de COD, le principal élément déterminant la couleur de l'eau dans cette région, avec une précision de l'ordre de 1 mg/L des concentrations observées, à l'aide des données du TM (r multiple = 0,93, $P < 0,01$). En dérivant les relations entre le pH, la couleur de l'eau et la concentration de COD, les données de Landsat fournissent un moyen de distinguer et de cartographier les lacs acides et les lacs non acides de la région étudiée. L'examen des caractéristiques de réflectance d'un seul lac acide (lac Bowland) qui a subi une neutralisation suggère qu'il est possible d'utiliser les données de Landsat pour détecter les changements des caractéristiques optiques au cours du temps. Toutefois, la capacité de surveiller la dimension temporelle de l'acidification des lacs par des données fournies par satellite n'a pas encore été établie.

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The acquisition of lake surface water samples for water quality assessments involves considerable expense in terms of monies, time, and effort. This is especially so, and may be prohibitive, if the objective is to undertake long-term monitoring of numerous lakes which are scattered over a large geographical area and where accessibility is difficult. Remote sensing, in conjunction with traditional forms of lake monitoring efforts, offers the capability of gathering data on at least some of the surface water parameters that are required in a relatively rapid, efficient, and economical manner.

When undertaken prior to standard lake survey methods, remote sensing results may then be used to guide the sampling programs of more intensive in situ surveys. They may also provide spatial and temporal information for a set of study lakes that is impossible to acquire in any other manner.

Northeastern Ontario provides an opportunity to test this capability. Located in the area is the world's largest, single point-source of sulphur dioxide emissions, the Sudbury nickel–copper smelting complexes of the Inco Metals Company and Falconbridge Nickel Mines Limited. The adverse effect of acidic deposition on the freshwater systems of the region is a major environmental concern that has long been recognized (Gorham and Gordon 1960; Beamish and Harvey 1972).

Over the past two decades, major changes in smelting processes, the adoption of pollution abatement measures, an extended strike, and numerous summer shutdown periods have substantially reduced airborne emissions. Associated with these reduced local emissions, and also perhaps due to altered provincial deposition patterns (Kelso and Jeffries 1988), lake water quality improvements have been observed, including increases in pH and alkalinity and decreases in sulphate, nickel, and copper concentrations (Keller and Pitblado 1986; Keller et al. 1986).

It is likely that some of the changes that have occurred within these lakes can be detected by image analysis techniques. The use of remotely sensed data for lake acidification studies has not always been successful (Hardy and Jeffries 1981; Moniteq 1982; see commentary by Bukata et al. 1982 and Pitblado 1984). On the other hand, based on work and data derived from a project sponsored by the Ontario Ministry of the Environment (MOE), significant advances towards this goal have been reported (Pitblado et al. 1987; Marshall and Tanis 1989;

Pitblado and Dempsey 1989; Pitblado 1992).

In this paper, digital satellite data are employed to demonstrate how one can discriminate between acidic and nonacidic lakes in a small study area northeast of the City of Sudbury, downwind from the nickel–copper smelting complexes. Empirical relationships, using multivariate statistical procedures, are established between satellite reflectance data and selected lake surface water parameters. In addition and as a step in determining the feasibility of using Landsat data for temporal analyses, preliminary discussions of the changes in reflectance (over the period 1973–86) of a single acidic lake (Bowland Lake) are reported.

Study Area

The region north of Lake Wanapitei (see Fig. 3A) is an area where field water quality assessments have been undertaken and where cloud-free, satellite digital data are available. Approximately 1000 km^2, this project area contains limnological and terrain features known to be representative of a significant portion of the Precambrian Shield and characteristic of the Sudbury region.

The lakes cover a broad spectrum of nutrient characteristics and levels of acidity. In terms of the latter feature, the study area contains a number of lakes which are known to be acidic ($pH < 5.5$) but the range in pH values that has been observed in field investigations extends from 4.3 to 7.5. Topography is generally rolling, with frequent showings of exposed bedrock and relatively minor, scattered, but locally important amounts of Quaternary deposits. The geology of the field location is dominated by quartzite formations with some granitic intrusives and metavolcanics (Fortescue and Stahl 1987). Less than 100 km downwind from the nickel–copper smelting complexes of Sudbury, this is a prime example of a region where atmospheric inputs of sulphur affect lakes situated in watersheds of moderate to low buffering capacity.

Bowland Lake (47°5′N, 80°50′W) is located a few kilometres to the north and west of the principal study area, some 70 km from Sudbury. In August 1983, it was treated with $CaCO_3$ as part of a long-term programme to investigate the feasibility of using neutralization as a means of protecting and rehabilitating Ontario lakes which receive high inputs of acid deposition (Keller et al. 1990). Prior to treatment, the mean pH value for Bowland Lake was 4.9. Soon after neutralization, values of whole-lake pH exceeded 6.0, reaching a maximum of 6.7 in the summer of 1984, and declining since that time (Molot et al. 1990).

Methods

Satellite Imagery

The Landsat-5 Thematic Mapper (TM) scanner records reflected and emitted radiation from the earth in seven bands of the electromagnetic spectrum. The wavelength bounds for channels in the visible portion of the spectrum are TM1 0.45–0.52 μm (blue-green), TM2 0.52–0.60 μm (green), and TM3 0.63–0.69 μm (red). In the near- and midinfrared the channels are TM4 0.76–0.90 μm (near), TM5 1.55–1.75 μm(mid), and TM7 2.08–2.35 μm (mid). All of these channels record information from an area (30 × 30 m) on the ground referred to as a pixel. Thermal data are also recorded (TM6 10.40–12.50 μm (far-infrared)) but for a much larger pixel area (120 × 120 m). Scanner data for each channel are in the form of digital numbers (DN) and range from 0 (zero radiance) to 255 (maximum radiance).

TABLE 1. Landsat scenes available for temporal analyses of Bowland Lake.

Scanner	Date (d-mo-yr)	Satellite
MSS	13-7-73	Landsat 1
MSS	8-8-75	Landsat 2
MSS	3-7-80	Landsat 3
MSS	20-7-82	Landsat 5
TM	20-6-84	Landsat 5
TM	1-8-85	Landsat 5
TM	22-5-85	Landsat 5
TM	13-8-86	Landsat 5
MSS	13-8-86	Landsat 5

The Sudbury area lakes north of Lake Wanapitei can be observed on TM satellite images from the scene identified as Path 19 - Row 27, using the Landsat World Referencing System. The cloud-free Landsat-5 image that was employed for this paper has the identification number 51247-153429, dated 31 July 1987. With the EASI PACE software of PCI Inc. (1989), a computer routine was written to remove atmospheric haze using the procedure suggested by Richards (1986), outline water bodies with a polygon border, and then compute and record the mean DN for each of the seven TM channels for each lake that was large enough to discriminate. In order to cover a reasonably large study area, the digital image was sampled at a ratio of 1:2, i.e. every other scan line and pixel. With this image decimation, very small ponds or lakes (most of which are less than 10 ha in surface area) were eliminated from the sampling protocol.

The analysis of Bowland Lake included data from both the Landsat TM and multispectral (MSS) scanners. The wavelength bounds for channels of the latter are, in the visible portion of the spectrum, MSS1 0.5–0.6 μm (green-yellow) and MSS2 0.6–0.7 μm (red) and, in the near infrared, MSS3 0.7–0.8 μm and MSS4 0.8–1.1 μm. To enable comparisons between the two scanners, the quantized and calibrated scaled radiance in DN units was transformed to spectral radiance (watts per square metre per steradian per micrometre) using the expressions provided by the Canada Centre for Remote Sensing (CCRS 1987). With the images listed in Table 1, temporal reflectance alterations of Bowland were examined by computing channel ratios. For the Landsat MSS and TM sensors, respectively, these were Green/Red: MSS1/MSS2, TM2/TM3; Green/NIR: MSS1/MSS4, TM2/TM4; and Red/NIR: MSS2/MSS4, TM3/TM4.

Lake Survey Data

The study area contains numerous water bodies, including wetlands with open water, ponds, rivers, and lakes. For this project, the sampling protocol for the satellite data and the availability of lake chemistry data from field surveys substantially reduced the number of lakes included in the investigation. Prime attention is given here to 70 lakes which have a surface area larger than 10 ha (see Fig. 3A; Fig. 3A was derived from the Landsat image but has not been registered to any map projection). For reference purposes, the following lakes have been identified: (a) Dougherty: 47°01′, 80°40′; (b) Paradise: 46°59′, 80°46′; (c) Chiniguchi: 46°57′, 80°42′; (d) Laura: 46°57′, 80°36′; (e) Wanapitei: 46°45′, 80°45′; (f) Kukagami: 46°44′, 80°33′; and (g) Maskinonge: 46°47′, 80°27′.

Slightly less than half of these lakes have been surveyed by traditional limnological methods which will allow for the comparisons of satellite predictions with field observations. As part of a larger, detailed lake sampling survey (Pitblado 1992), 27 lakes were sampled in August 1986. Water samples were collected in sample-rinsed, 4-L plastic jugs, as water column composites of the top 5 m of water for lakes of sufficient depth, and as surface grab samples (at 0.5 m below the surface) in shallow lakes. Visual colour observations, Secchi disc transparency, and bottom depth measurements were also made at this time. Sample separates were created and then sent to MOE laboratories in either Toronto or Thunder Bay for chemical analyses (analytical methods followed MOE 1981). As well as the 27 lakes sampled for this project, data were available for seven additional lakes in the study area. The data for these latter lakes were acquired by MOE (W. Keller, pers. comm.) and the Ontario Ministry of Natural Resources (D. Wales, MNR, Toronto, pers. comm.).

Statistical Analyses

Water colour and dissolved organic carbon (DOC) have been used in this paper to initially separate acidic from nonacidic lakes or to distinguish classes within the acidic lake group itself. As a number of such groupings were experimented with, the definitions of the various classes have been left to the sections below. Multivariate discriminant and regression techniques (Mather 1976; SPSS Inc. 1988) were employed with either water quality parameters or Landsat channels as predictor or independent variables. In these analyses, the Landsat channels that were employed included atmospherically corrected DN values for each TM band and various numerical transformations. Both absolute spectral radiance and channel ratio values have been employed for the discussion of reflectance changes for Bowland Lake: before, during, and after neutralization.

Results and Discussion

Early on in the use of remotely sensed data for water quality assessments, Swain and Davis (1978) strongly supported an earlier statement by Wezernak and Polcyn (1972) that "the occurrence of colored water deserves to be delineated and documented even if the observed phenomena are not immediately interpretable." That statement is equally applicable to the occurrence of clear or noncoloured waters. In the context of this paper, clear water may well flag a lake that has been acidified as a result of contamination by atmospheric pollutants (Almer et al. 1974; Yan 1983; Effler et al. 1985).

Visual Colour Discriminations

In 1986, colour designations were assigned in the field to 27 of the lakes contained within the study area by one observer (H. Stahl, formerly of the Ontario Geological Survey). The designations included terms such as blue, bluish green, greenish blue, brown, etc. For exploratory purposes, these visual colour codes were regrouped into three general categories: blue, green, and brown. With respect to the latter category, brown does not refer to "brown-water lakes" in the sense of swamps, bogs, or dystrophic lakes (Oliver et al. 1983).

Do these categories provide for water chemistry discriminations? If the visual colour categories provide meaningful water chemistry discriminations, can satellite reflectance data simulate this grouping of lakes which have been subjectively distinguished on the basis of colour groups? To answer the first question, 20 water chemistry parameters that were common to 25 of the lakes surveyed in 1986 were employed in a stepwise, multiple discriminant analysis. The analysis sought to identify the degree of separation of the three colour groups in terms of water chemistry and the variables which were most significant for their separation. Subsequently, to answer the second question, the Landsat reflectance parameters were employed to determine the degree of discrimination of these same categories of lakes.

In terms of water chemistry parameters, a classification success rate of 92% is indicated in Table 2. Only one of the lakes identified in the field as having a "blue" colour is misclassified; similarly, only one of the "green" lakes does not fall into the correct class. Based on the Landsat TM channels, 84% of the lakes fell into the correct colour class (Table 2). Once again the extreme ends of the colour scale (blue and brown) were the easiest to classify, with increased error in classification occurring in the green category. The source of errors may be derived from the regrouping of the colour codes, incorrect colour coding in the field (which might be improved, as suggested by a reviewer of an earlier draft of this paper, by adopting more standardized field procedures, e.g. the use of colour swatches), or an actual lack of association between water colour, water chemistry, and satellite reflectance measurements.

Eleven water chemistry and four Landsat variables are adequate to discriminate between the three groups of lakes that have been categorized by general visual colour codes ($P < 0.05$, using stepwise multivariate discriminant analyses). As Table 3 indicates, there are clear patterns established between the categories of lakes based on these colour designations. Three of the water chemistry variables decrease in value from the blue to brown classes of lakes: Secchi disc depth, Al, and Zn. The pH of these lakes and all of the remaining variables increase in value or in concentration. And all of the Landsat reflectance parameters decrease from the blue to the brown categories of lakes.

Based on these results, satellite imagery could be used as a large-area reconnaissance mapping tool to quickly identify these general groupings of lakes. It is recognized that the associations observed here are based on a very limited number of lakes in a relatively small portion of the province. Certainly not all acid lakes are clear or stand out on Landsat images as is the case for this study area. But one must also acknowledge that of the 250 000 lakes in Ontario, and possibly more than 500 000 (Cox 1978), water quality data are available for a minute fraction of them (see Neary et al. 1990). Even a coarse categorization such as this would be better than nothing at all and would provide a basis for more intensive in situ sampling programmes.

Dissolved Organic Carbon Predictions

The colour of lake waters is the product of incoming direct and diffuse solar radiation, selective scattering and absorption of that radiation by the water itself as well as the materials dissolved and suspended in it, and finally reflection. In chemical terms, colour is associated with dissolved humic and fulvic substances and suspended matter. For some authors (e.g. Wetzel 1975) the colour of lake water is almost exclusively equated with DOC concentrations. Neary et al. (1990) have recently provided a series of regression equations for Ontario lakes which relate colour (both apparent and true) with the concentrations of DOC. These parameters are highly correlated with each other, having r^2 values ranging from 0.575 to 0.888, depending on latitude, i.e. colour increases with an increase in the concentration of DOC. For the lakes examined in this paper,

TABLE 2. Discriminant classification results for lakes grouped by general visual colour codes.

Actual group	No. of lakes	Predicted group membership		
		Blue	Green	Brown
Discrimination based on the water chemistry parameters				
Blue	7	6 (85.7%)	1 (14.3%)	
Green	13	1 (7.7%)	12 (92.3%)	
Brown	5			5 (100.0%)
Discrimination based on the Landsat TM values				
Blue	7	6 (85.7%)	1 (14.3%)	
Green	13	1 (7.7%)	10 (76.9%)	2 (15.4%)
Brown	5			5 (100.0%)

TABLE 3. Mean parameter values by general water colour codes for the significant discriminating variables (standard deviations in parentheses).

Discriminating parameters	Water colour designations		
	Blue (n = 7)	Green (n = 13)	Brown (n = 5)
DOC (mg/L)	0.3 (0.2)	1.6 (1.2)	3.3 (0.4)
Chlorophyll *a* (μg/L)	0.3 (0.1)	1.2 (1.2)	2.0 (0.6)
Secchi depth (m)	8.5 (2.2)	5.9 (2.8)	4.4 (0.6)
pH	4.60 (0.3)	5.34 (1.0)	5.76 (0.9)
TIP alkalinity (mg/L)	−1.56 (0.9)	0.57 (3.4)	1.20 (2.3)
Total P (μg/L)	3.0 (0.8)	4.9 (3.2)	6.4 (1.4)
Ca (mg/L)	1.9 (0.6)	2.9 (1.2)	3.0 (0.8)
Na (mg/L)	0.5 (0.1)	0.7 (0.1)	0.8 (0.1)
Al (μg/L)	324 (133)	218 (220)	112 (101)
Fe (μg/L)	45 (12)	55 (23)	158 (90)
Zn (μg/L)	10 (2)	8 (4)	7 (5)
TM1 (blue-green)	14.6 (3.5)	11.2 (3.2)	7.1 (1.1)
TM4 (near-infrared)	11.2 (3.1)	11.2 (3.1)	9.1 (0.7)
TM5 (midinfrared)	9.0 (3.0)	8.6 (2.8)	6.8 (0.5)
TM7 (midinfrared)	3.3 (1.2)	3.2 (1.1)	2.7 (0.3)

suspended mineral and chlorophyll *a* concentrations are very low (Pitblado 1992) and it is felt contribute little to the water colour of the study lakes.

In studies of acidic and nonacidic lakes using remotely sensed data, these colour–DOC relationships are extremely important. In particular, Almer et al. (1974), Yan (1983), and Effler et al. (1985) have demonstrated alterations in transparency (Secchi disc depth) which accompany lake acidification and neutralization. Increases in transparency with acidification have been observed in association with a depletion of DOC, perhaps due to coagulation/adsorption by Al and subsequent losses from the water column (Effler et al. 1985). And water clarity has been identified as a parameter that is routinely capable of being determined using satellite data (Brooks 1975; Alföldi and Munday, Jr. 1977).

For the study lakes examined for this paper, with the exception of a small number of outliers, there is a strong association ($r = 0.78$, $P < 0.001$) between pH and DOC concentrations (Fig. 1). This is accompanied by a significant ($P < 0.01$) inverse association between DOC concentrations and Secchi disc depth, when both of these parameters have been transformed to common logarithms. The latter association is relatively weak ($r = -0.48$) for this small number of lakes; but when they are included with the larger number of Sudbury Environmental Study or Atmospheric Precipitation in Ontario Study lakes (Pitblado et al. 1980; Keller and Pitblado 1986; Keller et al. 1986), they are located in the "bend" of the strongly asymptotic trend of decreasing Secchi depth with increasing DOC. And to lend further support to the colour–DOC–Al link (Effler et al. 1985), mean values for Secchi depth and Al decrease (Table 3) across the series of blue-green-brown lakes outlined above, while pH and DOC concentrations increase.

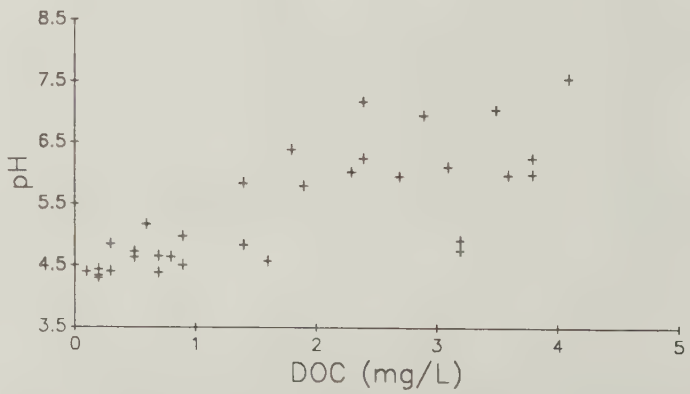

FIG. 1. Scatterplot showing the relationship between DOC and pH in the study area.

To determine whether Landsat TM data could be used to predict the DOC concentrations of the study lakes, a stepwise

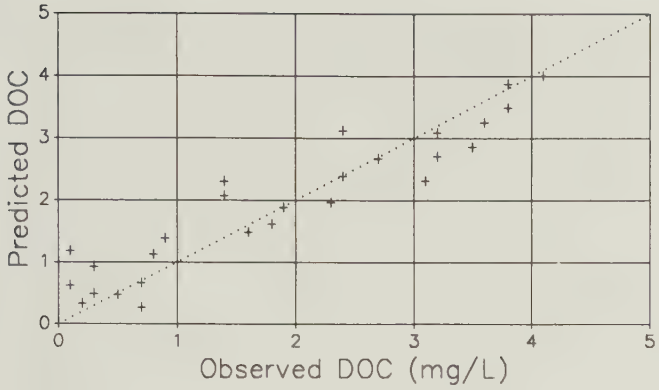

FIG. 2. Observed versus predicted DOC concentrations.

multiple regression analysis was undertaken. Using data from the 27 lakes surveyed in 1986, the association was derived by employing DOC as the dependent variable and the DN values from the TM channels as the independent variables. The resulting regression equation is shown below (multiple $r = 0.93$, $P < 0.01$):

$$(1)\quad \mathrm{DOC} = 8.86 - 4.31 \cdot \mathrm{LG10\,(TM1)} - 0.87 \cdot \mathrm{TM2} + 1.36 \cdot \mathrm{TM3} - 2.13 \cdot \mathrm{TM4}^{0.5}.$$

For these 27 lakes plus the additional seven MOE/MNR lakes, the observed concentrations of DOC range from 0.1 to 4.1 mg/L (Fig. 2), with a mean of 1.7 mg/L and a standard deviation of 1.32 mg/L. This is the range of DOC within which the majority of Ontario lakes fall (Neary et al. 1990). The comparable minimum, maximum, mean, and standard deviation for the predicted DOC concentrations are 0.10, 4.01, 1.67, and 1.22 mg/L, respectively. The greatest,absolute difference between observed and predicted DOC was 1.08 mg/L. A 1 mg/L grid has been used in Fig. 2 to show that the majority of the predictions fall within the same (observed–predicted) 1 mg/L category and never exceed one category.

If Landsat data can be used to predict DOC with reasonable accuracy and if DOC can be used as a surrogate measure of other lake parameters such as pH (see Fig. 1), then Landsat data should be used as a water quality mapping tool. To illustrate that capability, the regression model (Eq. 1) was applied to all of the lakes shown in Fig. 3A. The range of predicted DOC was divided into five categories (Fig. 3B–3F).

Results of this mapping exercise exceeded expectations. Every one of the known acidic lakes in the study area was located (i.e. all of the lakes in Fig. 3B). And the known pH values, along with DOC concentrations, for the lakes in the remaining panels increase from Fig. 3C to 3F. It would be reasonable to expect that the lakes for which no current field data are available have also been mapped correctly.

The methodological approach adopted for this study raises two major concerns. The first is the well-known fact that the empirical, multivariate statistical approach to remote sensing water quality assessments is often image and date dependent (e.g. see Lindell 1986; Lindell et al. 1986). Unfortunately, the alternative "modelling" approach using radiative transfer theory requires a battery of instrumentation that was not available for this analysis and assumes that the theory has been developed sufficiently to be operational. The latter is clearly not the case. In discussing some of the absorption measurements necessary for the functioning of radiative transfer models, Smith and Baker (1981, p. 177) stated that "there is less discrepancy among the later data, although the agreement is not as good as

FIG. 3. Landsat TM (A) location map of the study lakes and (B–F) spatial distribution of lakes by Landsat-predicted DOC (mg/L): (B) 0.0–1.0; (C) 1.1–2.0; (D) 2.1–3.0; (E) 3.1–4.0; (F) >4.0.

the published accuracies would suggest. As a consequence, there is still uncertainty in the choice of the most reliable data set." In Canada, both the successes and failures of this approach can be seen with work reported from the Canada Centre for Inland Waters (e.g. Bukata et al. 1985; Jerome et al. 1989). In the long term, operational water quality monitoring tools will be derived through a combination of continuing empirical and modelling research efforts.

The second concern relates to the pH–DOC associations presented here. The strong link between pH and DOC shown in Fig. 1 may well be characteristic of only anthropogenetically acidified lakes. Statements about this relationship for Precambrian Shield lakes generally are beyond the scope of the present case study. On the other hand, a weaker but similar relationship has been observed using 230 lakes scattered throughout northeastern Ontario (Pitblado 1992). The latter area receives annual sulphur depositions which are significantly less than that for the immediate Sudbury region but greater than that for northwestern Ontario, i.e. lakes in the sulphur deposition Zones 3 (0.50–0.75 g $S \cdot m^{-2} \cdot yr^{-1}$), 4 (0.75–1.00 g $S \cdot m^{-2} \cdot yr^{-1}$), and 5 (1.00–1.25 g $S \cdot m^{-2} \cdot yr^{-1}$) of Neary et al. (1990).

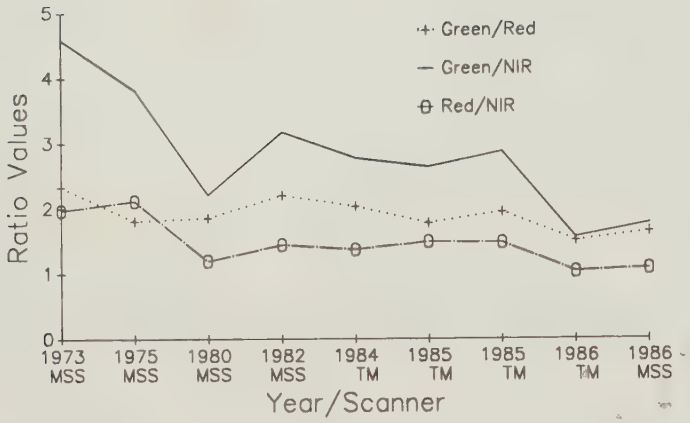

FIG. 4. Bowland Lake reflectance ratios for selected Landsat images from 1973 to 1986.

Monitoring Prospects

Based on the success of the results presented here in terms of using satellite data as a mapping tool, one is lead to consider the capability of Landsat data for temporal analyses. Bowland Lake was selected for this test because of the availability of both Landsat and water chemistry data for times before, during, and after neutralization.

In addition to the pH alterations referred to earlier, Molot et al. (1990) have provided evidence of statistically significant increases in DOC. They also speculated that the change in DOC could have accounted for the decrease in Secchi disc depth from means of 7.8 m (preneutralization period June 1982 – July 1983) to 5.4 m (postneutralization period May 1984 – October 1985).

It is clear that neutralization has, among other things, altered the optical characteristics of Bowland Lake. What is not so clear is whether Landsat has the resolution capable of detecting these changes.

Remote sensing studies of terrestrial targets have made extensive use of channel ratios as a means to compare data from different times and different satellites (e.g. see the vegetation distribution and change detection studies for the Sudbury area: Pitblado and Amiro 1982; Allum and Dreisinger 1986). The use of channel ratios has met with some success for water quality analyses (Piech et al. 1978; Jerome et al. 1989), but Novo and Godoy, Jr. (1989) were unable to detect trophic level changes in a Brazilian reservoir for the period from 1984 to 1988 using TM reflectance ratios. In work done for the present project on lakes in the Lake Wanapitei area, it has been observed that the Green/Red ratios of acidic lakes are always higher than those of nonacidic lakes.

The Bowland Lake channel ratios (Fig. 4) provide tantalizing evidence for changes in reflectance over the period from 1973 to 1986. As one would expect, the reflectance ratios decrease over time as the pH and DOC increase and the Secchi disc depth decreases (Molot et al. 1990). The sharp decreases in Fig. 4 for the 1980 and 1986 ratio values are primarily due to the presence of haze or light cloud over or in the proximity of Bowland that could not be eliminated.

In addition to this visual inspection of the plotted channel ratios, discriminant function (comparing all Bowland Lake pixel values by year) and a series of linear correlation (relating channel ratios by year) analyses were undertaken with the cloud- and haze-affected images removed. Only a 66% level of discriminant classification accuracy could be achieved. And while the linear correlation coefficients confirmed the trend of decreasing ratio values over time (e.g. for the Green/Red ratio, $r = -0.80$), they were not statistically significant.

At this stage in the analysis, the Bowland Lake reflectance data only suggest that changes in the optical characteristics of the lake are being sensed by Landsat. It must be noted that the difference in DOC reported by Molot et al. (1990) is less than the ± 1 mg/L prediction capabilities of the regression equation used in the previous section of this paper. In the upper strata of the lake, the mean concentrations of DOC increased from 2.0 mg/L (June 1982 – July 1983) to 2.5 mg/L (August 1983 – October 1985). It is at this point where radiative transfer modelling may play a significant role in resolving the question of Landsat capabilities for temporal water quality monitoring.

Conclusions

For the Sudbury area lakes, clear relationships exist between water quality parameters (or groups of parameters) and water colour, and satellite sensors can measure water colour – DOC with sufficient sensitivity to discriminate beween acidic and nonacidic lakes. However, the empirical relationships that have been determined in this paper may not be appropriate in areas where lake colours are dominated by constituents other than DOC. The capability for monitoring the temporal dimension of lake acidification using satellite data has yet to be established.

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References

ALFÖLDI, T. T., AND J. C. MUNDAY, JR. 1977. Progress toward a Landsat water quality monitoring system. Proceedings, p. 325–340. 4th Canadian Symposium on Remote Sensing, Quebec, May 16–18.

ALLUM, J. A. E., AND B. R. DREISINGER. 1986. Remote sensing of vegetation change near Inco's Sudbury mining complexes. Int. J. Remote Sens. 8: 399–416.

ALMER, B., W. DICKSON, C. EKSTROM, E. HORNSTROM, AND U. MILLER. 1974. Effects of acidification on Swedish lakes. Ambio 3: 30–36.

BEAMISH, R. J., AND H. H. HARVEY. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BROOKS, D. J. 1975. Landsat measures of water clarity. Photogramm. Eng. Remote Sens. 40: 1269–1272.

BUKATA, R. P., J. E. BRUTON, AND J. H. JEROME. 1982. The futility of using remotely-determined chlorophyll concentration to infer acid stress in lakes. Can. J. Remote Sens. 8: 38–41.

1985. Application of direct measurements of optical parameters to the estimation of lake water quality indicators. Scientific Series No. 140, National Water Research Institute, Environment Canada, Burlington, Ont. 35 p.

CCRS (CANADA CENTRE FOR REMOTE SENSING). 1987. MOSAICS: multiobservational satellite image correction system. Energy Mines Resour. Can. Tech. Inf. Package, Ottawa, Ont. 9 p.

COX, E. T. 1978. Counts and measurements of Ontario lakes. Ont. Minist. Nat. Res. Rep., Toronto, Ont. 93 p. plus appendices.

EFFLER, S. W., G. C. SCHAFRAN, AND C. T. DRISCOLL. 1985. Partitioning light attenuation in an acidic lake. Can. J. Fish. Aquat. Sci. 42: 1707–1711.

FORTESCUE, J. A. C., AND H. STAHL. 1987. Geochemical survey of the Sturgeon River area, Districts of Sudbury and Timiskaming. Ont. Geol. Surv. Geochem. Ser. Map 80 799, Toronto, Ont.

GORHAM, E., AND A. G. GORDON. 1960. The influence of smelter fumes upon the chemical composition of lake waters near Sudbury, Ontario, and upon the surrounding vegetation. Can. J. Bot. 38: 477–487.

HARDY, N. E., AND W. C. JEFFERIES. 1981. Chromaticity analysis of color aerial photography and its application to detection of water quality changes in acid-stressed lakes. Can. J. Remote Sens. 7: 4–23.

JEROME, J. H., J. E. BRUTON, AND R. P. BUKATA. 1989. Optical monitoring of water quality in inland waters. Proceedings, Vol. 5, p. 2799–2803. 12th Canadian Symposium on Remote Sensing, Vancouver, July 10–14.

KELLER, W., D. P. DODGE, AND G. M. BOOTH. 1990. Experimental lake neutralization program: overview of neutralization studies in Ontario. Can. J. Fish. Aquat. Sci. 47: 410–411.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water Air Soil Pollut. 29: 285–296.

KELLER, W., J. R. PITBLADO, AND N. I. CONROY. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. Water Air Soil Pollut. 31: 765–774.

KELSO, J. R. M., AND D. S. JEFFRIES. 1988. Response of headwater lakes to varying atmospheric deposition in north-central Ontario, 1979–85. Can. J. Fish. Aquat. Sci. 45: 1905–1911.

LINDELL, L. T. 1986. Operational water quality surveillance in Sweden using Landsat MSS data. Proceedings, p. 385–394. 10th Canadian Symposium on Remote Sensing, Edmonton, May 5–8.

LINDELL, L. T., B. KARLSSON, M. ROSENGREN, AND T. ALFÖLDI. 1986. A further development of the chromaticity technique for satellite mapping of suspended sediment load. Photogramm. Eng. Remote Sens. 52: 1521–1529.

MARSHALL, E. J., AND F. J. TANIS. 1989. Spatial and spectral characterization of acid rain stress in Canadian Shield lakes. Proceedings, Vol. 5, p. 2808–2810. 12th Canadian Symposium on Remote Sensing, Vancouver, July 10–14.

MATHER, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons Inc., London.

MOE (ONTARIO MINISTRY OF THE ENVIRONMENT). 1981. Outlines of analytical methods. Tech. Rep., Toronto, Ont. 246 p. plus appendices.

MOLOT, L. A., P. J. DILLON, AND G. M. BOOTH. 1990. Whole-lake and nearshore water chemistry in Bowland Lake, before and after treatment with $CaCO_3$. Can. J. Fish. Aquat. Sci. 47: 412–421.

MONITEQ. 1982. Evaluation of historical Landsat data on water reflectance for acidic precipitation applications in the Sudbury area. Monitoring Environmental Quality Ltd., Concord, Ont.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ont. Minist. Environ. Rep., Dorset, Ont. 146 p. plus appendices.

NOVO, E. M. L. M., AND M. GODOY, JR. 1989. Eutrophication assessment through remote sensing techniques. Proceedings, Vol. 5, p. 2825–2828. 12th Canadian Symposium on Remote Sensing, Vancouver, July 10–14.

OLIVER, B. G., E. M. THURMAN, AND R. L. MALCOLM. 1983. The contribution of humic substances to the acidity of colored natural waters. Geochim. Cosmochim. Acta 47: 2031–2035.

PCI INC. 1989. EASI/PACE user's manuals. PCI Inc., Richmond Hill, Ont.

PIECH, K. R., J. R. SCHOTT, AND K. M. STEWART. 1978. The blue-to-green reflectance ratio and lake water quality. Photogramm. Eng. Remote Sens. 44: 1303–1310.

PITBLADO, J. R. 1984. Monitoring the impacts of airborne pollutants with digital remote sensing: progress and prospects in the Sudbury area. Laurentian Univ. Rev. 16: 67–79.

1992. The mapping of lake surface water characteristics of Northeastern Ontario using satellite imagery. Res. Technol. Branch, Ont. Minist. Environ. Project No. 354G Rep., Toronto, Ont. 157 p. plus appendices.

PITBLADO, J. R., AND B. D. AMIRO. 1982. Landsat mapping of the industrially disturbed vegetation communities of Sudbury, Canada. Can. J. Remote Sens. 8: 17–28.

PITBLADO, J. R., AND D. A. DEMPSEY. 1989. What does an acidic lake "look" like? Oper. Geogr. 7: 20–23.

PITBLADO, J. R., W. KELLER, AND N. I. CONROY. 1980. A classification and description of some Northeastern Ontario lakes influenced by acid precipitation. J. Great Lakes Res. 6: 247–257.

PITBLADO, J. R., F. J. TANIS, AND W. A. WOITOWICH. 1987. Remote sensing and the monitoring of lake acidification in Northeastern Ontario, Canada: preliminary observations, p. 364–371. *In* R. Perry, R. M. Harrison, J. N. B. Bell, and J. N. Lester [ed.] Acid rain: scientific and technical advances. Selper Ltd., London.

RICHARDS, J. A. 1986. Remote sensing digital image analysis. Springer-Verlag, New York, NY.

SMITH, R. C., AND K. S. BAKER. 1981. Optical properties of the clearest natural waters (200–800 nm). Appl. Opt. 20: 177–184.

SPSS INC. 1988. SPSS-X user's guide. SPSS Inc., Chicago, IL.

SWAIN, P. H., AND S. M. DAVIS [ED.] 1978. Remote sensing: the quantitative approach. McGraw-Hill Inc., New York, NY.

WETZEL, R. G. 1975. Limnology. W. B. Saunders, Philadelphia, PA.

WEZERNAK, C. T., AND F. C. POLCYN. 1972. Eutrophication assessment using remote sensing techniques. Proceedings, Vol. 1, p. 541–551. 8th International Symposium on Remote Sensing of Environment. Environmental Research Institute of Michigan, Ann Arbor, MI.

YAN, N. D. 1983. Effects of changes in pH on transparency and thermal regimes of Lohi Lake, near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 40: 621–626.

Phytoplankton of Sudbury Area Lakes (Ontario) and Relationships with Acidification Status

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Phytoplankton data from samples collected in July 1981 from 111 lakes in the Sudbury area were analyzed by canonical community ordination analysis and other techniques to reveal associations of taxa which were related to environmental gradients among the lakes. Phytoplankton data from a group of seven lakes sampled in the mid-1970's or early 1980's and in the mid-1980's were analyzed for evidence of temporal change. In both data sets, factors related to trophic status and acidification status were inferred to be important controlling variables. For example, desmid genera fell into two general groupings, one typical of clear-water, nutrient-poor, low-alkalinity lakes (e.g. species of *Micrasterias, Bambusina, Euastrum, Spondylosium*) and the other representing lakes higher in nutrients and alkalinity (e.g. species of *Teilingia, Closterium, Xanthidium, Staurastrum*). This latter group also included several chlorophytes (*Ulothrix, Schroederia, Scenedesmus*) and euglenoids (*Euglena, Phacus*). Well-defined relationships existed between lake alkalinity, pH, and total numbers of phytoplankton taxa. The smaller data set included lakes subjected to recent decreases in acid deposition and corresponding increases in pH over a 10-yr interval, and the increased numbers of phytoplankton taxa were indicative of recovery from earlier acidification.

Les données sur le phytoplancton obtenues sur des échantillons prélevés en juillet 1981 dans 111 lacs de la région de Sudbury ont été étudiées par analyse canonique d'ordination des communautés ainsi que par d'autres techniques afin de mettre en évidence les associations de taxons reliées à des gradients environnementaux dans les lacs. Les données sur le phytoplancton obtenues sur un groupe de sept lacs échantillonnés au milieu des années 1970 ou au début et au milieu des années 1980 ont été analysées afin d'y déceler des preuves d'un changement temporel. Dans les deux ensembles de données, on a supposé que les facteurs reliés à l'état trophique et à l'état d'acidification étaient des variables déterminantes. Par exemple, les desmidiées se divisaient en deux catégories générales, l'une caractéristique des lacs transparents, pauvres en éléments nutritifs et à faible alcalinité (p.ex. espèces de *Micrasterias, Bambusina, Euastrum, Spondylosium*), l'autre représentant les lacs à alcalinité et à teneur en éléments nutritifs plus élevées (p.ex. espèces de *Teilingia, Closterium, Xanthidium, Staurastrum*). Ce dernier groupe incluait également plusieurs chlorophytes (*Ulothrix, Schroederia, Scenedesmus*) et des eugléniens (*Euglena, Phacus*). Il existait des relations bien définies entre l'alcalinité du lac, son pH et le nombre total de taxons du phytoplancton. L'ensemble de données plus petit incluait des lacs ayant connu récemment une diminution des dépôts acides et une augmentation correspondante du pH sur un intervalle de 10 ans, et le nombre accru de taxons composant le phytoplancton était indicateur d'une récupération par rapport à l'acidification passée.

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Since the recognition of anthropogenic acid deposition as a major impact on lake ecosystems in Scandinavia and northeastern North America, acidification effects on phytoplankton have been examined in laboratory simulations, experimental enclosures, comparative lake studies, synoptic multilake surveys, and long-term whole-lake acidification and neutralization experiments (see reviews by Geelen and Leuven 1986; Stokes 1986; Weatherley 1988). The earliest results were somewhat inconclusive with respect to certain effects on phytoplankton (e.g. whether or not production and biomass were influenced by acidification). Recent data clearly demonstrate that phytoplankton production and biomass are controlled by the supply of limiting nutrients (Havens and DeCosta 1984; Kerekes et al. 1990). Factors such as metal toxicity, especially Al (Paul and Nalewajko 1984; Havens and DeCosta 1987; Pillsbury and Kingston 1990), zooplankton grazing (McCauley and Briand 1979), and competition for low levels of dissolved inorganic carbon (Williams and Turpin 1987) act indirectly and variably to control biomass and composition of the phytoplankton of acidic lakes. Loss of species from the phytoplankton is a major effect of lake acidification (see reviews by Geelen and Leuven 1986; Stokes 1986; Minns et al. 1990).

The Sudbury area of central Ontario includes many lakes which have been impacted by acidic deposition from metal smelting operations. The phytoplankton of some of these lakes has been studied over a number of years (Yan 1979; Yan and Miller 1984) and includes observations of changes induced by whole-lake neutralization with base additions (Yan and Dillon 1984; Molot et al. 1990). Recent reductions in sulphur dioxide emissions from the Sudbury smelters have been related to

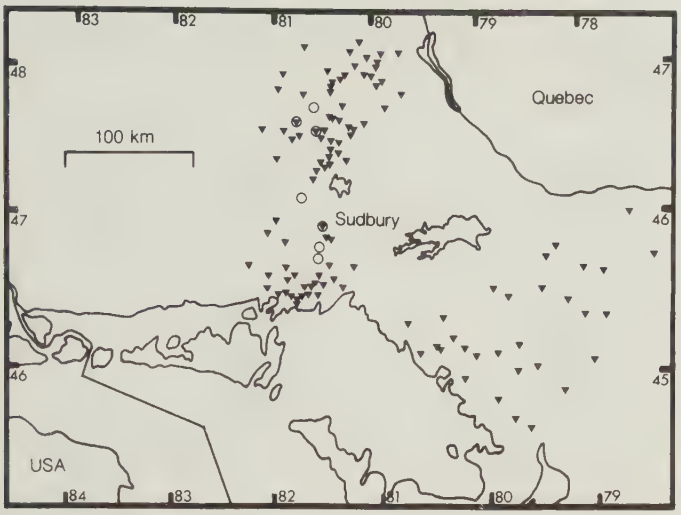

FIG. 1. Map of the study area showing the location of the lakes. The larger lake set (111 lakes) is marked with solid triangles and the smaller lake set (seven lakes) with open circles. Three lakes are common to both data sets.

increases in alkalinity and declines in metals (Dillon et al. 1986; Hutchinson and Havas 1986; Keller and Pitblado 1986) and recovery of planktonic rotifer and crustacean populations (MacIsaac et al. 1986; Keller and Yan 1991) as well as recovery of other biota of Sudbury area lakes (Keller et al. 1992). There have been no previously published synoptic phytoplankton surveys of Sudbury area lakes. The only evidence so far for recovery of phytoplankton communities in response to SO_2 emission decreases is for siliceous algae (diatoms and scaled chrysophytes) for which paleolimnological methods have been used (Dixit et al. 1989).

Phytoplankton samples were collected from 111 of 250 lakes that constituted part of a large synoptic survey of water quality within a 260-km radius of Sudbury (Pitblado and Keller 1984; Keller and Pitblado 1986). In addition, seven lakes were sampled more intensively (weekly or bimonthly) during the ice-free season of several years from 1974 to 1986. Our objectives were to determine (1) if there were patterns in the phytoplankton communities related to acidification status in the larger lake set and (2) if significant changes in phytoplankton community structure had occurred in the seven lakes over time.

Methods

Of the 250 lakes sampled between mid-June and mid-August 1981, samples for phytoplankton were collected from 111 of these (Fig. 1; Appendix 1) for which visits to lakes could be confined to a short time period in midsummer (between July 6 and July 21) in order to minimize the effect of seasonality. The locations, morphometric data, and watershed characteristics of all lakes are provided in Pitblado and Keller (1984) and for the seven more extensively sampled lakes in Keller and Yan (1991).

Phytoplankton samples from the 111 lakes were collected through the euphotic zone in the deepest part of each lake using a weighted tygon tube lowered to a depth of twice the Secchi disc visibility plus 1 m. Samples from Whitepine Lake in 1980–81 and Sans Chambre Lake were also collected as non-volume-weighted tygon tube composites. Samples from Whitepine Lake during 1982–86 and from Joe and Swan lakes were collected as euphotic zone composites volume-weighted according to the contribution of different lake strata to the lake volume. Samples from Welcome, Wavy, and Laundrie lakes were taken by lowering and raising a weighted sample bottle at a uniform rate through the euphotic zone. Samples were fixed immediately with Lugol's iodine solution (I – KI – glacial acetic acid) and preserved with formalin after concentration by sedimentation in the Ontario Ministry of the Environment's Toronto laboratory.

Phytoplankton analyses on samples collected since 1976 have followed Nicholls and Carney (1979), using inverted microscopy, Utermöhl-type counting chambers, and expression of phytoplankton "density" as cell volume. There was, therefore, consistency in the 111-lake set, but the seven-lake set contained some results (pre-1976) from a very different analytical protocol (compound microscopes with Sedgewick–Rafter chambers). A decision was made to reanalyze the preserved samples in 1986 as pooled composites of the ice-free period. Only a subset of the original 1970's collections was selected for this purpose so that results would be comparable with those from the 1980's when lakes were sampled monthly and samples were also pooled before analyses. This procedure was also intended to remove bias relating to the (presumed) enhancement of analytical expertise over time (potentially important with respect to changes in numbers of taxa over time). Several individual samples (not pooled) from the 1970's collections were reanalyzed in 1986 by the old method (Sedgewick–Rafter cell) to confirm the adequacy of preservation over the approximately 10-yr interval. No consistent differences which could be related to a possible preservation problem were found.

Most of the identifications were made to the level of genus (Appendix 2); however, some more easily identified species were recorded (e.g. *Peridinium inconspicuum* (= syn. *P. umbonatum*), *P. limbatum, P. wisconsinense*), while others were grouped at levels above genus (e.g. unidentified "naked" Dinophyceae). Some taxa with suspected autecological differences were also distinguished (e.g. *Chrysochromulina breviturrita* and *C. parva*). Taxa were grouped under seven classes and compiled in ASCII format for PC use with statistical and plotting programmes (SYSTAT v. 4.0 and 5.0; CANOCO v. 2.1 (ter Braak 1988); Freelance v. 3.01).

Multivariate community analysis techniques based on older methods such as multiple linear regression models are often inadequate to define species – environmental variable relationships because these models assume linear relationships, which in reality are more likely to be unimodal (ter Braak and van Dam 1989). Canonical correspondence analysis (CCA; applied with the computer programme "CANOCO"; ter Braak 1988) is a unimodal statistical model which has clear advantages over other multivariate analysis techniques (ter Braak and van Dam 1989). It was used here to identify the relative positioning of assemblages of phytoplankton taxa along environmental gradients in the CCA ordination field. Lakes and phytoplankton taxa were simultaneously ordinated relative to the ordination axes which were constrained to be linear combinations of the environmental variables.

For comparative purposes, and to help in detecting patterns in phytoplankton community composition, a community classification method based on a dendrogram of assemblage dissimilarity values as well as a nonmetric multidimensional scaling ordination ("SYSTAT" statistical software package; Wilkinson 1988) were applied to the species by lake matrix.

Because the input of all taxa from all lakes in multidimensional scaling ordination resulted in an unworkably large data matrix (111 × 121), two separate routines were followed to reduce the data set by about 25%. First, the lakes were arranged

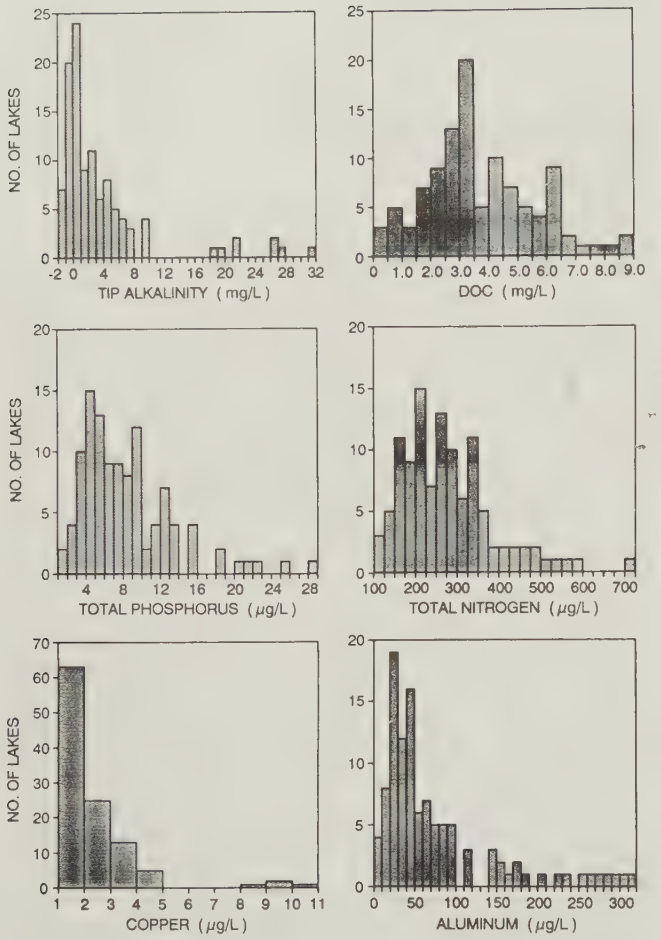

FIG. 2. Frequency distributions for ranges of chemical variables in the 111-lake set. *Note*: total inflection point (TIP) alkalinity does not include one outlier at 94 mg/L.

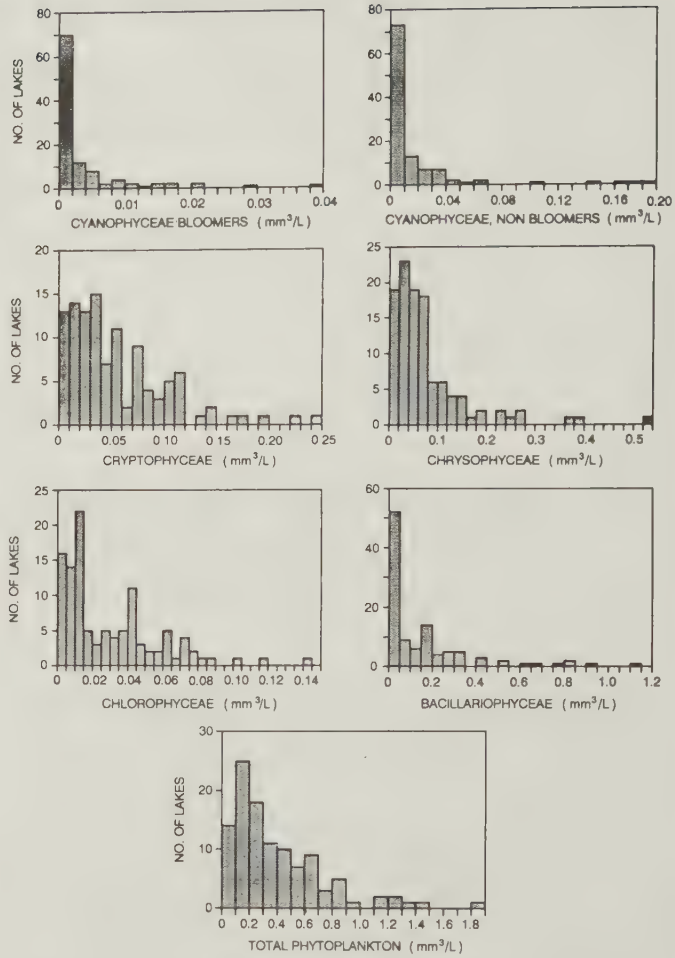

FIG. 3. Frequency distributions for density (biovolume) ranges of total phytoplankton and the dominant classes in the 111-lake set. *Note*: blue-green "nonbloomers" were predominantly species of *Merismopedia, Aphanothece, Chroococcus, Rhabdoderma* and *Aphanocapsa*, while "bloomers" were mainly species of *Anabaena, Aphanizomenon, Lyngbya, Oscillatoria, Microcystis, Coelosphaerium*, and *Gomphosphaeria*.

in order according to their alkalinity values and every third lake was deleted. The other procedure involved the arbitrary removal of 30 lakes from the middle range of the lake alkalinity/frequency distribution (alkalinity = 0–3.9 mg/L), thus retaining all of the lakes with the lowest and the highest alkalinities for the ordination. In a few cases, where environmental data were not available from the 1981 survey, data from 1982, 1983, or from Regional Ontario Ministry of the Environment files for the late 1970's were used. Water chemistry sampling methods have been described by Pitblado and Keller (1984).

Results

111-Lake Set

Chemistry

Of the six major limnological variables considered (alkalinity, dissolved organic carbon (DOC), total phosphorus, total nitrogen, copper, aluminum), only DOC showed a normal distribution among the lakes. The data set included several lakes with high concentrations of copper and aluminum which resulted in skewed frequency distributions of these variables (Fig. 2). In general, the most frequent ranges of chemical variables (representing approximately 70% of all lakes) were as follows: alkalinity, 2–4.5 mg/L; DOC, 1.8–6.2 mg/L; total phosphorus, 3–10 μg/L; total nitrogen, 150–350 μg/L; copper, 1–2.8 μg/L; aluminum, 15–100 μg/L.

Phytoplankton

Most lakes were low in total biovolume, reflecting their nutrient-poor, oligotrophic status. The most frequent ranges (representing approximately 70% of all lakes) were as follows: total phytoplankton, 0.05–0.65 mm^3/L; Bacillariophyceae, 0.05–0.2 mm^3/L; Chrysophyceae, 0.01–0.09 mm^3/L; Cryptophyceae, 0.005–0.06 mm^3/L; Cyanophyceae (nonbloomers), 0.005–0.015 mm^3/L; Cyanophyceae (bloomers), <0.001–0.003 mm^3/L; Chlorophyceae, 0.002–0.05 mm^3/L (Fig. 3). These data do not include a few "outliers." For example, Lake 147 (Erables) with 0.148 mm^3 Cyanophyceae bloomers/L, Lake 16 (Raft) with 0.34 mm^3 Chlorophyceae/L, Lake 45 (Eagle) with 1.6 mm^3 Bacillariophyceae/L, and Lakes 54, 143, and 242 (Laura, Klock, and Little Laundrie) with 1.31, 0.47, and 0.53 mm^3 Dinophyceae/L, respectively.

Euglenophyceae were poorly represented in the lake set. *Trachelomonas, Euglena*, and/or *Phacus* species were recorded from only six lakes. Five of these lakes had relatively high total nitrogen and total phosphorus levels (301–561 μg N/L and 13–22 μg P/L), and four were highly coloured (38–65 Hazen units). Dinophyceae were widely distributed (present in 93 of the lakes), but with the few exceptions noted above, biovolumes were very low (<0.011 mm^3/L in 57% of these lakes). Dino-

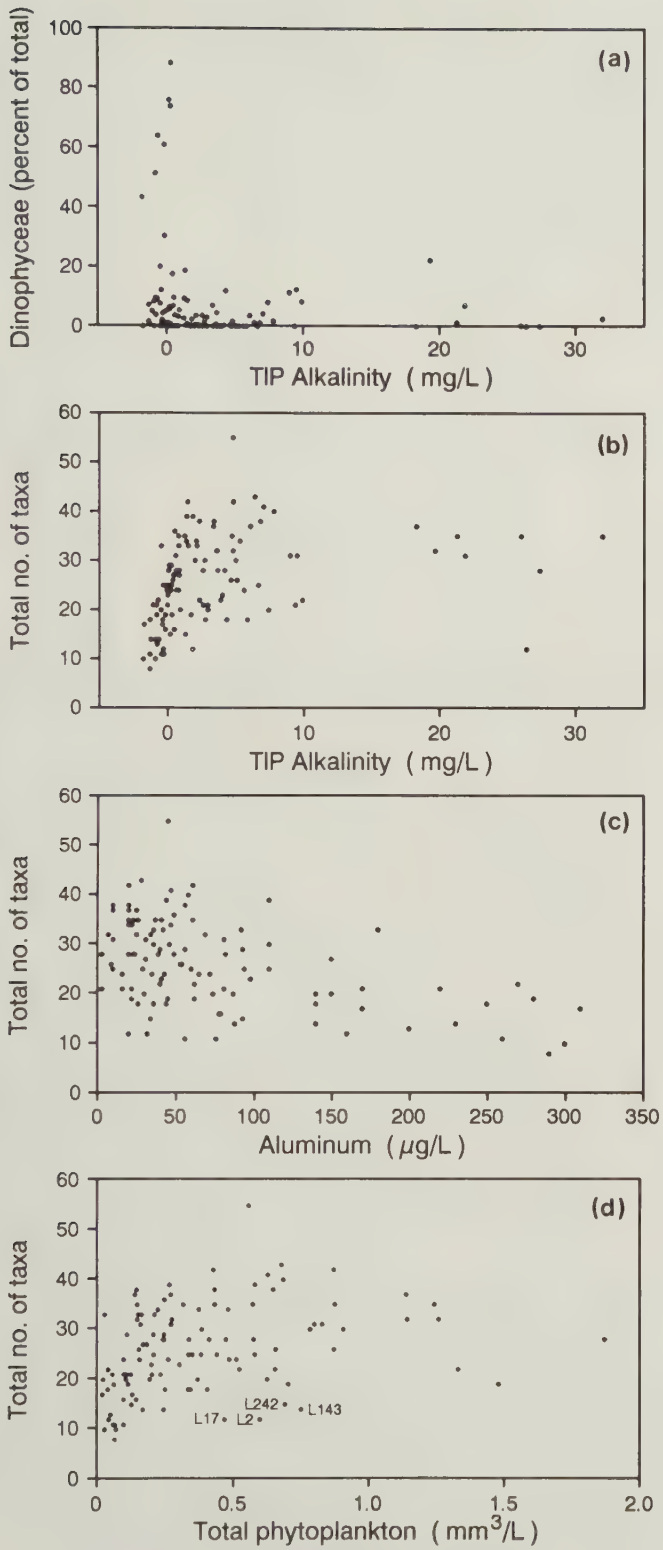

FIG. 4. Relationships among phytoplankton and alkalinity or aluminum in the 111-lake set. (a) Dinophyceae (as a percentage of total phytoplankton biovolume) and lake alkalinity; (b) total number of phytoplankton taxa and lake alkalinity; (c) total number of phytoplankton taxa and total aluminum concentration; (d) total number of phytoplankton taxa and total phytoplankton volume ($r = 0.303$). A few lakes may be outliers for reasons relating to atypical combinations of physicochemical features, e.g. Lake 17 was extremely high in total dissolved salts (conductivity = 264 µS; $Cl^- = 44$ mg/L) and Lake 143 was shallow (7 m) and high in aluminum (100 µg/L).

flagellates were a major part of the total phytoplankton community only in lakes with very low alkalinities (Fig. 4a). The reverse was true for other algal groups and for total phytoplankton biovolume, where positive correlations were observed with lake alkalinity (over the restricted range −2 to 10 mg/L) and total phosphorus concentrations, but negative correlations were observed with aluminum levels (Table 1).

Total numbers of phytoplankton taxa ranged from lows of 8, 10, and 10 in Lakes 50, 94, and 71 (Chiniguchi, Florence, and Nellie) to a high of 55 in Lake 203 (Mowat). The maximum numbers of taxa for the major classes were 20 Chlorophyceae, 13 Chrysophyceae, 9 Bacillariophyceae, 8 Cyanophyceae, 4 Dinophyceae, 3 Cryptophyceae, and 3 Euglenophyceae. Alkalinity, total phosphorus, and aluminum were the three most important factors related (linearly) to the numbers of phytoplankton taxa (Table 1; Fig. 4b, 4c). It is clear that the alkalinity/number of taxa relationship is best defined over the low-alkalinity range (Fig. 4b). This may also be true of the influence of total phytoplankton biovolume on the total number of taxa, where total biovolumes above 1.0 mm^3/L did not contribute linearly to the relationship (Fig. 4d).

The CCA produced a sample (lake) biplot (Fig. 5) in which the ordination axes were defined by the environmental variables such that each variable was represented by an arrow pointing in the direction of maximum change within the lake set. The longer the arrows, the more highly correlated with the axes are the variables. The most important environmental variables in the 111-lake set (in defining the relative positions of the lakes in the ordination field) were total nitrogen, colour, total phosphorus, and alkalinity. Aluminum and Secchi disc visibility were also important but were negatively related to the four previously listed variables. This is to be expected both on the basis of intuition (i.e. the most acidic, nutrient-poor lakes are clear-water lakes, highest in aluminum) and on the basis of the linear correlation coefficients (Table 1).

Phytoplankton taxa were ordinated within the same set of environmental axes (Fig. 6) and revealed some interesting relationships. For example, *Peridinium* sp. and *P. limbatum* favoured clearer waters higher in aluminum and lower in alkalinity than *P. wisconsinense* and *P. inconspicuum*. Virtually all of the bloom-forming blue-green algal genera (*Aphanizomenon, Microcystis, Gomphosphaeria, Coelosphaerium, Lyngbya, Oscillatoria*) were grouped in the lower left quadrant (Fig. 6), while *Merismopedia, Chroococcus*, and *Rhabdoderma* were located in the upper right quadrant (clearer water, higher metals, lower alkalinity, lower nutrients). Several desmid genera (*Micrasterias, Bambusina, Euastrum, Spondylosium*) were all located in the lower right quadrant (clear water, low alkalinity). In contrast, other desmids (*Teilingia, Closterium, Xanthidium*) along with several chlorophytes (*Ulothrix, Schroederia, Scenedesmus*) and euglenophytes (*Euglena, Phacus*) clearly favoured lakes higher in nutrients and alkalinity.

Algae associated with high aluminum levels included species of *Tabellaria, Chrysolykos, Mallomonas, Cryptomonas, Chrysochromulina, Rhabdoderma, Paramastix, Chrysosphaerella, Navicula, Asterionella*, and *Chrysococcus*. Taxa with a low apparent tolerance for metals (and higher nutrient requirements?) include all of the bloom-forming blue-green algae mentioned above and *Bicosoeca, Trachelomonas, Planctonema, Gomphonema, Stauroneis, Coelastrum, Tetrastrum, Eudorina*, and *Dictyosphaerium*. It is noteworthy that the three *Chrysosphaerella* taxa recorded (*C. longispina, C. corona circumspina*, and *Chrysosphaerella* sp. (probably *C. brevispina*) showed a well-defined positioning along the aluminum gradient

TABLE 1. Linear correlation coefficients (r values) for biovolume and numbers of taxa of the dominant phytoplankton classes and total phytoplankton versus total phosphorus, alkalinity, aluminum, and copper concentrations in the 111-lake set. Asterisks show significance at the 95% confidence level.

	TP (μg/L)	TIP alkalinity (mg/L)		Al (μg/L)	Cu (μg/L)
		Entire range[a]	−2 to 10 mg/L		
Biovolume (mm^3/L)					
Cyanophyceae	0.232*	0.039	0.334*	−0.207	−0.166
Bloomers	0.208*	0.081	0.231*	−0.169	−0.072
Nonbloomers	0.176	0.008	0.286*	−0.165	−0.161
Dinophyceae	−0.086	−0.041	−0.085	−0.074	−0.058
Cryptophyceae	0.238*	0.338*	0.270*	−0.328*	0.159
Chrysophyceae	0.089	0.007	0.149	−0.175	0.009
Chlorophyceae	0.329*	0.251*	0.189	−0.236*	0.279*
Bacillariophyceae	0.291*	0.225*	0.454*	−0.302*	−0.001
Total phytoplankton	0.314*	0.237*	0.421*	−0.400*	0.011
No. of taxa					
Cyanophyceae	0.194	0.061	0.450*	−0.539*	−0.250*
Dinophyceae	0.040	0.155	0.025	0.120	0.047
Cryptophyceae	0.227*	0.227*	0.463*	−0.608*	−0.116
Chrysophyceae	−0.008	−0.049	0.094	−0.232*	−0.109
Chlorophyceae	0.334*	0.148	0.362*	−0.350*	−0.037
Bacillariophyceae	0.311*	0.260*	0.553*	−0.492*	−0.008
Total	0.281*	0.176	0.457*	−0.480*	−0.101

[a]The entire alkalinity range (−2 to 32 mg/L) does not include Lake 173 (Shining Tree) with an alkalinity of 94 mg/L.

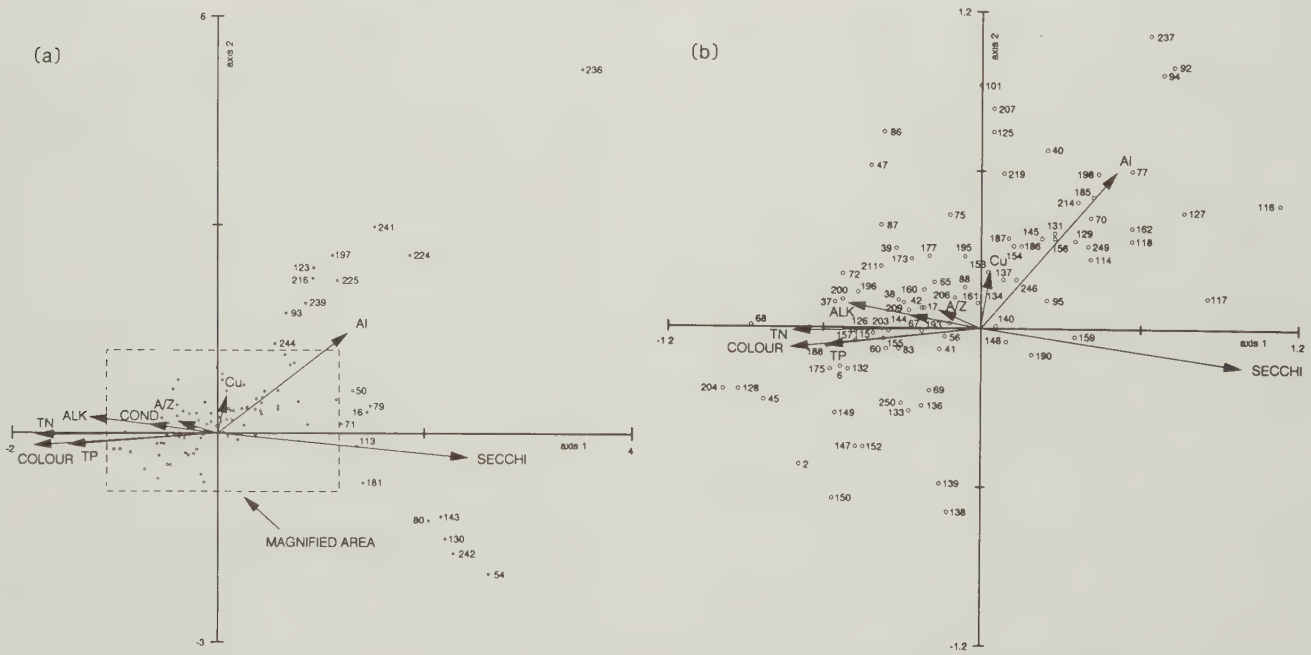

FIG. 5. (a) Locations of lakes within the CCA ordination field with axes defined by major environmental variables (A/Z = ratio of lake area to maximum depth; ALK = alkalinity; COND = specific conductance (25°C); TN = total nitrogen; TP = total phosphorus). (b) Magnified area of lake locations near the origin in Fig. 5a. Lake numbers are keyed in Appendix 1.

(Fig. 6). Two colonial chrysophytes recorded as *Uroglena* (no. 48) and *Uroglenopsis* (No. 49), which are likely two (or more) species of the genus *Uroglena*, also showed very different apparent tolerances to aluminum (Fig. 6).

Several well-defined groupings of lakes were identified by cluster analyses (Fig. 7) using a measure of dissimilarity of lake phytoplankton communities. For example, lakes with the most dissimilar phytoplankton communities (those clustered near the top of the dendrogram, above "C" in Fig. 7) had, with a few exceptions (Lakes 2, 113, 225, and 54), some of the highest alkalinities in the data set. Also, there were three small subsets of lakes, A, B, and C (Fig. 7), apparently with relatively similar (within-group), but distinctive (between-group) phytoplankton communities. Group A lakes were all acidic lakes with negative alkalinities; group B lakes were poorly buffered, but all had alkalinities >0; group C lakes (with the exception of Lake 65 with alkalinity = 27.4 mg/L) all had moderately low alkalinities. The average alkalinities of all three groups of lakes (−0.89, 1.25, and 4.7 mg/L, respectively) were all highly significantly different (paired Student's t-tests, $\alpha = 0.001$).

Nonmetric multidimensional scaling (MDS) ordinations were also helpful in identifying gradients among the lakes. Of the two reduced data sets used for MDS, only the set which retained all lakes with extreme alkalinities (see Methods) is illustrated

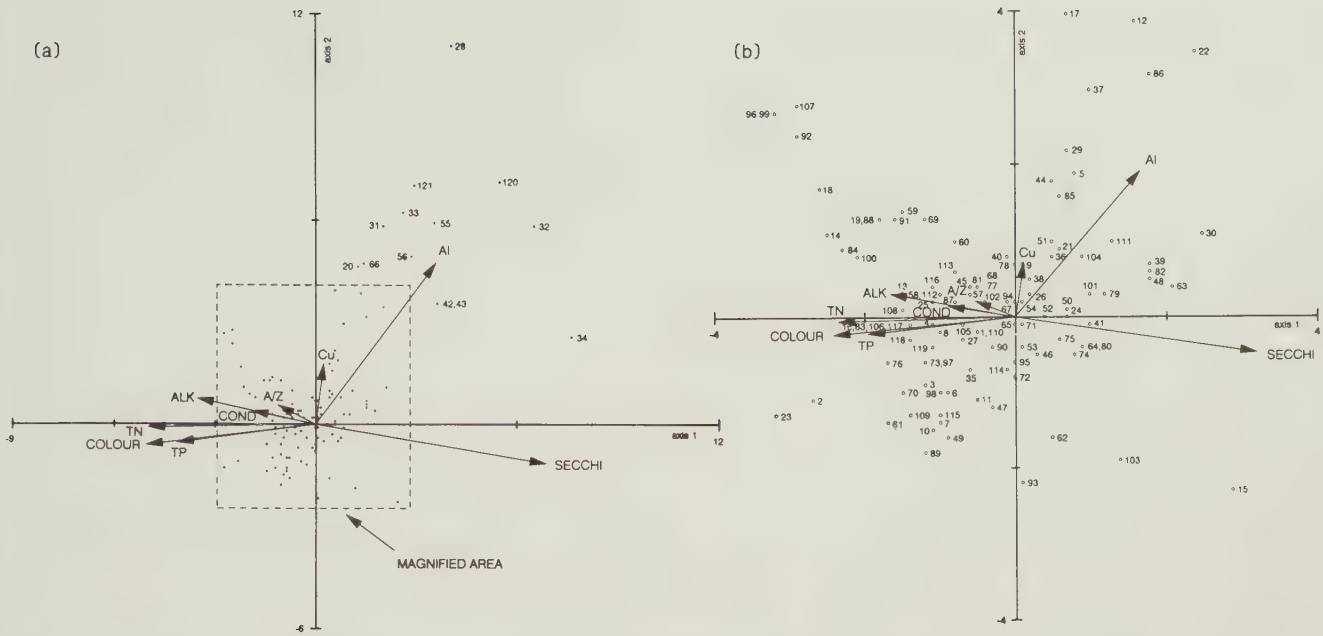

FIG. 6. (a) Locations of phytoplankton taxa within the CCA ordination field with axes defined by major environmental variables. (b) Magnified area of taxon locations near the origin in Fig. 6a. Taxon numbers are keyed in Appendix 2.

here (Fig. 8), since there were similarities in the two ordinations. Two apparent gradients were identified: one with Lakes 45 and 225 as the end points and the other with Lakes 175 and 242 as the end points (Fig. 8). Since these were roughly parallel to the first and second ordination axes, respectively, the axis scores for the lakes were regressed against the major environmental variables. Statistically significant correlations ($\alpha = 0.05$) were found for colour and total phosphorus, but not for alkalinity, aluminum, or several other variables.

Seven-Lake Set

Reliable alkalinity data are not available for the 1970's, but pH data suggest that Welcome Lake had the highest acid-neutralizing capacity of the seven lakes and Swan Lake the lowest (Table 2). Significant increases in pH occurred in all lakes except Welcome Lake and were accompanied by declines in copper, nickel, and aluminum concentrations (see table 2 of Keller and Yan 1991).

Total phytoplankton biovolumes were consistently two to three times higher in Swan Lake than in the other six lakes, where biomass ranged approximately between 0.20 and 0.45 mm^3/L (Table 2). In 1976, Laundrie Lake (Stations 2 and 3) had higher biovolumes in the 0.55–0.65 mm^3/L range. No consistent trends over time were observed except in Welcome and Wavy lakes, where mid-1980's biovolumes were considerably higher than in the mid-1970's (Table 2).

At the class level, there were major changes observed over the study period. These included a nearly universal increase in the relative abundance of Chrysophyceae (Fig. 9) and either marked declines in the combined relative abundance of Dinophyceae and Chlorophyceae, as for Swan and Laundrie lakes or an increase in Dinophyceae and Chlorophyceae, as for Joe and Welcome lakes (Fig. 9). Increases in these classes were at the expense of the Bacillariophyceae.

Total numbers of phytoplankton taxa increased markedly over time in Whitepine, Laundrie, Welcome, Wavy, and Joe lakes (Fig. 10). Swan and Sans Chambre lakes did not reveal a similar increase, but samples from before 1977 from Swan Lake and 1980 from Sans Chambre Lake were not collected. Total numbers of taxa increased by about 65, 20, and 65% in Laundrie, Welcome, and Joe lakes, respectively. Most of these increases were attributable to species of Chlorophyceae and Chrysophyceae. A highly significant linear correlation (Fig. 11) existed between the total number of phytoplankton taxa recorded and lake pH for the seven-lake set (all years).

A detailed evaluation of all taxonomic changes was done for only Joe, Laundrie, and Welcome lakes by comparing the changes in abundance of all recorded taxa with the taxon–alkalinity axis of the CANOCO analysis done on the 111-lake set. There do not appear to be simple explanations for the observed changes in phytoplankton. These three lakes showed increased representation by between 21 and 34 taxa and declines in only one to three taxa. The inferred controlling influences of alkalinity and several nutrient-related variables could not be separated on the basis of the CANOCO analyses. In Welcome Lake, for example, 70% of the taxonomic changes were predictable along the alkalinity and nutrient-related CANOCO axes. Because there was no significant change in the pH of Welcome Lake from the mid-1970's to the mid-1980's, it must be assumed that nutrient/trophic status factors were responsible for these taxonomic changes. Four taxa in the Welcome Lake phytoplankton were not included in this analysis (*Gloeotila, Cryptaulax, Chrysamoeba, Chrysidiastrum*) because they were not recorded in the original CANOCO analysis of the 111-lake set. Increases in five other taxa in Welcome Lake (*Chroococcus, Gomphosphaeria, Rhabdoderma, Chrysochromulina parva, Chrysosphaerella longispina*) suggested some increased recent influence of aluminum; however, aluminum concentrations in Welcome Lake did not increase over this period (Keller and Yan 1991).

In Joe Lake, the 1975 phytoplankton was dominated by species of *Dinobryon* and *Asterionella*. These species were much less important in 1985 and 1986 as were species of *Uroglena, Arthrodesmus, Botryococcus*, and *Chrysochromulina breviturrita*. The 1980's community was dominated by the diatoms *Cyclotella* and *Rhizosolenia* and low densities of many other

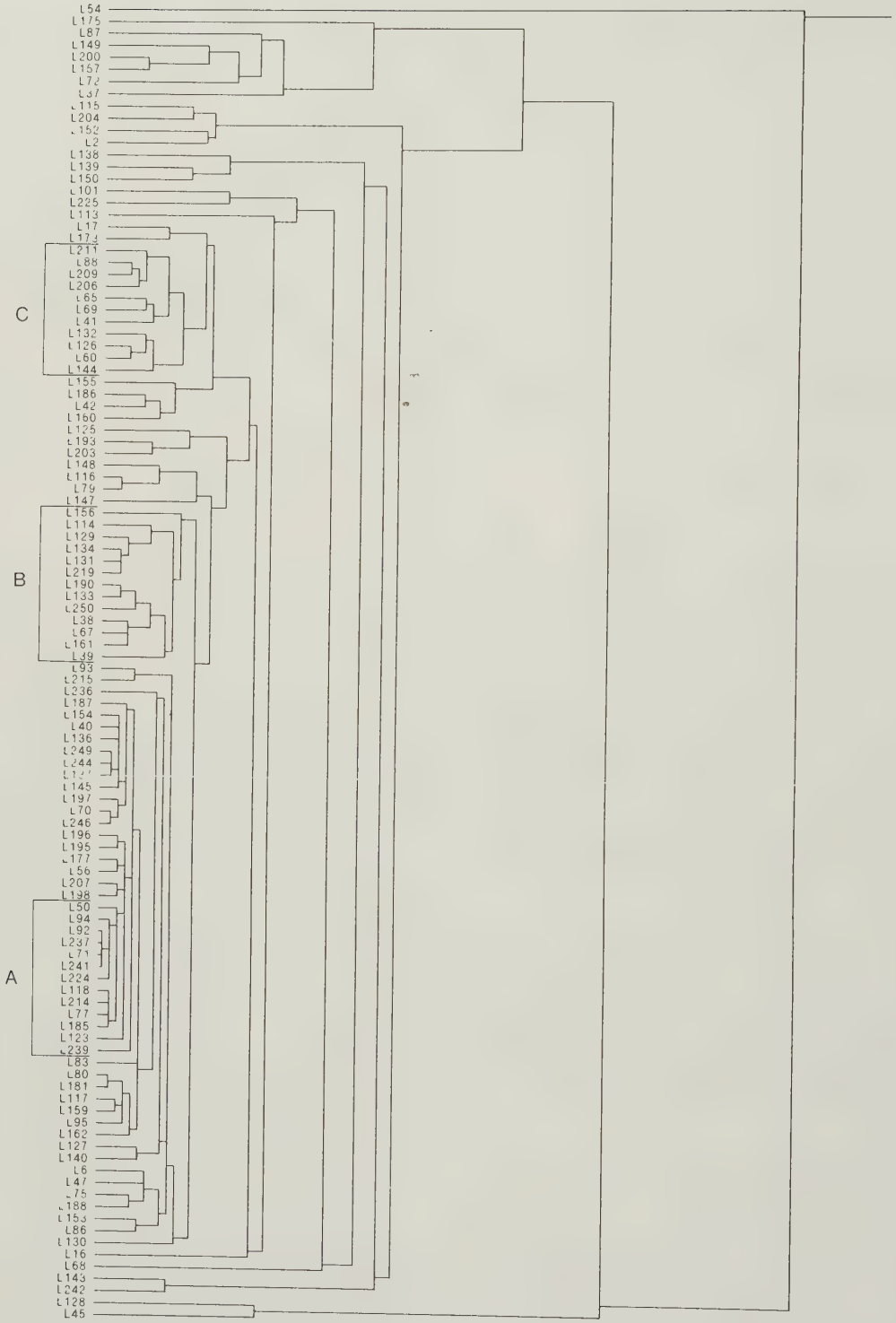

FIG. 7. Dendrogram (complete linkage method) of lakes based on phytoplankton dissimilarities calculated for all possible pairs of lakes (lakes are identified in Appendix 1). See text for explanation of A, B, and C.

taxa representing several classes, especially the Chlorophyceae (including desmids) and the Chrysophyceae.

In contrast with Welcome Lake, Joe Lake's aluminum concentrations declined from an average of 70 μg/L in 1975–76 to 19 μg/L in 1985–86 (Keller and Yan 1991). The only taxa showing significant declines in Joe Lake over this time period (*C. breviturrita, Asterionella, Dinobryon* spp.) were all closely related to the aluminum axis of the CANOCO analysis (111-lake set). A total of 34 other taxa showed increased representation. Of these, 75% were consistent with the alkalinity axis of the 111-lake set CANOCO analysis (after omission of seven taxa not included in the CANOCO analysis).

Wavy Lake was the only other lake (in addition to Welcome Lake) where trophic state changes were considered to be more important than changes in acid status. Total phytoplankton biomass increased sharply in 1985 over 1974 levels at all three

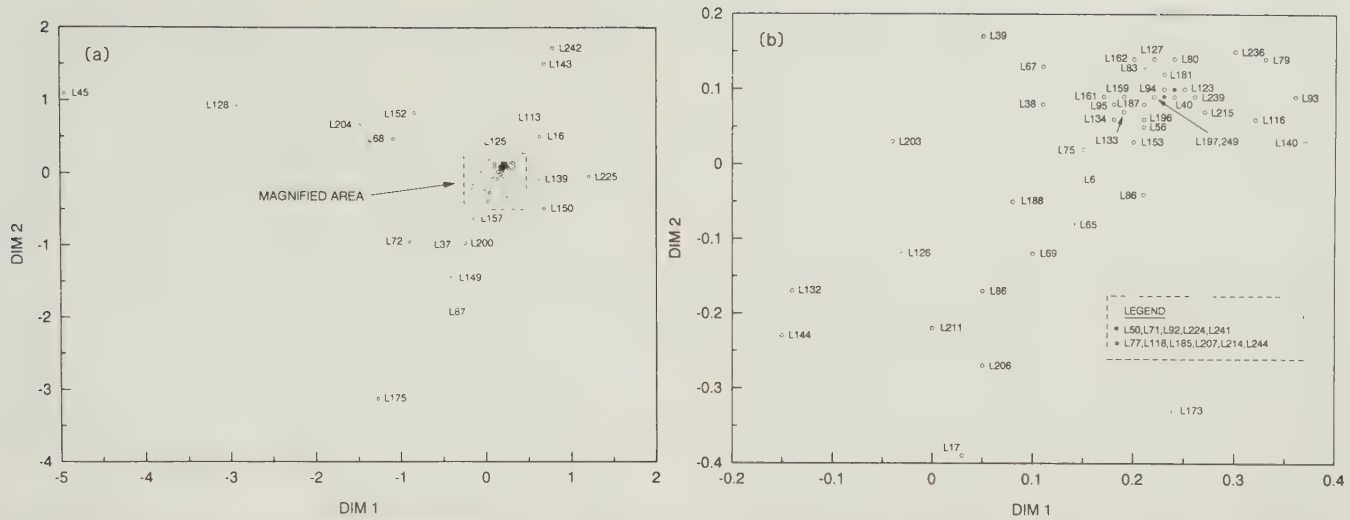

FIG. 8. (a) Locations of lakes within a two-dimensional MDS ordination field based on measures of dissimilarity of the phytoplankton communities calculated for all possible pairs of lakes. (b) Magnified area of lake locations within the ordination field in Fig. 8a.

Wavy Lake stations and then dropped to an intermediate level in 1986 (Table 2). The pH of Wavy Lake held constant at 4.7 in both 1985 and 1986, while the total number of taxa declined from the 1985 high of about 25 taxa to about 22 in 1986 (Fig. 10), thus mirroring the total biovolume changes. The total numbers of phytoplankton taxa in 1974 in Wavy Lake (averaging only about 18 for all three stations) were the lowest recorded numbers of all seven lakes and were consistent with both its extremely low pH (4.7) and its low total phytoplankton biovolume (averaging only 0.06 mm^3/L).

Discussion

Several recent studies have attempted to determine the effects of lake acidification and other factors on phytoplankton by synoptic surveys of large numbers of lakes and associated multivariate analyses of environmental variables (Earle et al. 1986, 1987; Morling and Willén 1990; Pinel-Alloul et al. 1990). Although canonical community ordination analysis is now widely used in paleolimnology for developing relationships between environmental factors and silica-scaled chrysophyte and diatom components in lake sediments (e.g. Dixit et al. 1989), CANOCO has been applied to phytoplankton data only twice previously (Fangström and Willén 1987; Willén et al. 1990). The output as species and site "biplots" displayed along environmental gradients offers relatively straightforward interpretation and considerable potential for further application to phytoplankton data. Even at the rather coarse level of data input undertaken in this study (mostly genus level identifications), several clear associations of algal taxa with trophic state and acidification-related variables emerged.

The most significant finding, however, was the existence of well-defined relationships between numbers of phytoplankton taxa and alkalinity for the 111-lake set and numbers of taxa and pH for the seven-lake set. Along with the lack of a relationship between total phytoplankton biovolume and alkalinity, these findings are consistent with recent experimental work on whole-lake acidification (Findlay and Kasian 1990), with several other regional studies of phytoplankton in lakes affected to various degrees by acidification (Almer et al. 1974; Kwiatkowski and Roff 1976; Dillon et al. 1979; Raddum et al. 1980; Hörnström and Ekström 1986), and with predictive models of species loss (Minns et al. 1990). While most of the previously published conclusions regarding loss of species richness with acidification have resulted from synoptic surveys, the seven-lake set reported here is one of the few examples of a time series study (in this case, about 10 yr) where phytoplankton response has been determined as a direct response to lake "deacidification." Alkalinity additions by whole-lake liming operations have also achieved similar recoveries of phytoplankton species richness (Eriksson et al. 1983; Weatherley 1988; Molot et al. 1990); however, these responses have been measured in "artificially" recovered systems over short periods (1–3 yr). Only in one other study, in western Sweden where lakes have been subjected to decreased acid deposition, has "natural" recovery of the phytoplankton been documented (Morling and Willén 1990). Interestingly, in the Swedish study, evidence for recovery in their "Phase III" lakes was based on minor shifts in taxonomic composition, and with regard to acidified lakes, the authors concluded that "acidification did not markedly change the number and composition of the phytoplankton, which to some degree diverges from earlier results presented in the literature."

In our larger (111 lakes) data set, there were associations or subsets of lakes with highly similar phytoplankton community structure which may have been determined by water chemistry (groupings of low-alkalinity lakes were distinguishable from other groupings of high-alkalinity lakes). However, there were enough exceptions to this within the entire data set to preclude any generalization about an overall relationship between phytoplankton structure and lake alkalinity. This probably was a consequence of the lack of species identifications. For example, it is now well known that several species of *Mallomonas* are distinctly alkaliphilous, while several other species are acidophilous (Siver and Hamer 1990). By not identifying *Mallomonas* and other genera to the species level, we undoubtedly have lost some resolution in the phytoplankton composition – environmental gradient analysis.

The CCA of the 111-lake set did not resolve phytoplankton associations responding to trophic state (total biovolume) changes and those responding to alkalinity changes because the directions of major influence of these variables in the ordination field were nearly identical. However, the seven-lake set included Welcome lake, a reference lake with circumneutral pH that experienced no change in acid-neutralizing capacity. In Welcome Lake, 70% of the shifts in taxonomic composition were

TABLE 2. May–October average total phytoplankton biovolume and "average" lake pH (calculated from H^+ concentrations) in the seven Sudbury area lakes.

Lake	Year	Biovolume (mm^3/L)	pH	No. of taxa
Joe				
Stn. 1	1975	0.448	5.7	34
	1985	0.342	6.2	50
	1986	0.376	6.3	54
Stn. 2	1975	0.448	5.7	31
	1985	0.265	6.2	48
	1986	0.402	6.3	49
Laundrie				
Stn. 1	1975	0.254	4.9	25
	1976	0.283	4.8	34
	1985	0.339	5.5	47
	1986	0.256	5.6	54
Stn. 2	1975	0.223	4.9	26
	1976	0.529	4.9	33
	1985	0.300	5.4	41
	1986	0.310	5.6	55
Stn. 3	1975	0.304	5.1	29
	1976	0.630	5.1	20
	1985	0.294	6.0	48
	1986	0.424	6.0	51
Sans Chambre	1980	0.340	5.4	25
	1981	0.349	5.4	37
	1983	0.143	5.8	38
	1985	0.352	5.9	33
Swan	1977	0.867	4.0	20
	1982	0.567	4.8	23
	1983	0.727	5.0	20
	1984	1.089	5.1	23
	1985	0.808	5.2	25
	1986	1.257	5.7	23
Wavy				
Stn. 1	1974	0.066	4.4	19
	1985	0.441	4.8	27
	1986	0.252	4.7	22
Stn. 2	1974	0.044	4.5	19
	1985	0.477	4.7	22
	1986	0.183	4.7	22
Stn. 3	1974	0.069	4.4	15
	1985	0.338	4.7	27
	1986	0.194	4.7	20
Welcome				
Stn. 1	1975	0.236	6.9	42
	1976	0.213	6.7	57
	1985	0.438	6.9	58
	1986	0.320	6.9	70
Stn. 2	1975	0.252	6.8	48
	1976	0.289	6.7	54
	1985	0.440	6.9	66
	1986	0.403	6.9	58
Whitepine	1980	0.498	5.5	33
	1981	0.295	5.7	25
	1982	0.376	5.8	36
	1983	0.356	5.8	45
	1984	0.307	5.8	43
	1985	0.338	5.8	50
	1986	0.143	5.9	38

predictable on the basis of the nutrient/trophic status axes in the CANOCO analysis. This was substantiated by the observed increase in total phytoplankton biomass of 68% at Station 1 and 56% at Station 2 between the mid-1970's and the mid-1980's.

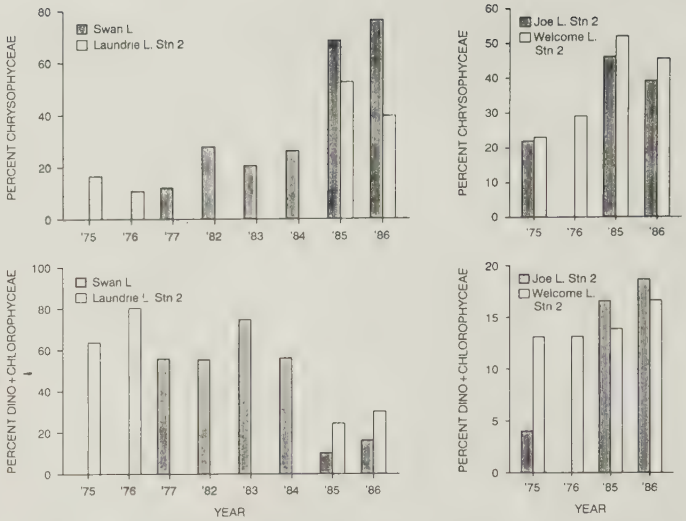

FIG. 9. Changes in the relative contributions of Chrysophyceae and Dinophyceae + Chlorophyceae in Swan, Laundrie, Joe, and Welcome lakes between 1975 and 1986.

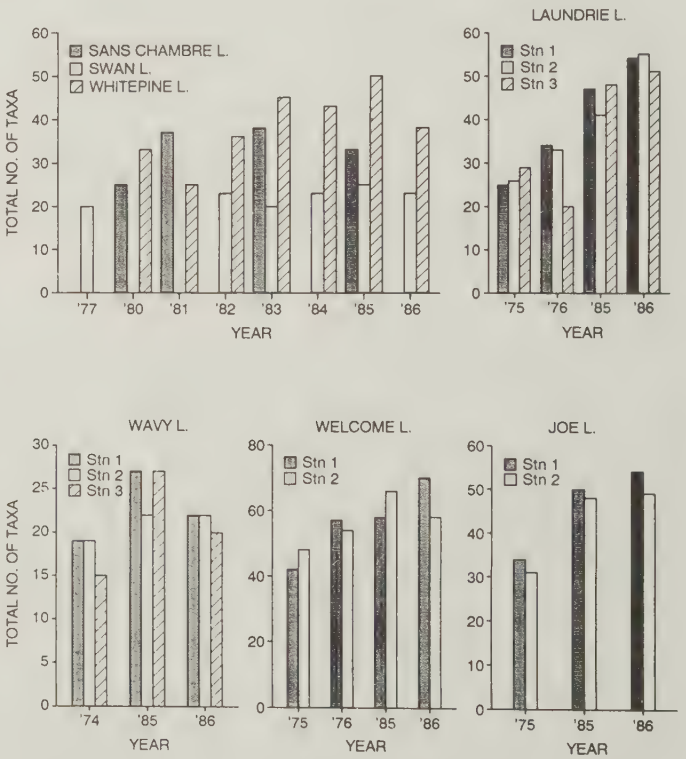

FIG. 10. Changes in the total numbers of phytoplankton taxa in seven Sudbury area lakes over approximately a 10-yr period.

Similarly, in Wavy Lake species richness closely followed total phytoplankton biovolume over the 3-yr period of observation of all three sampling sites. In general, however, total biovolume was not a significant copredictor of species richness for the entire seven-lake data set ($n = 52$, all stations, all years), undoubtedly because of the overriding influence of the changes in alkalinity. In a multiple linear regression analysis including only alkalinity and biovolume as independent variables, alkalinity contributed more than 80% of the total multiple coefficient of determination ($R^2 = 0.710$).

Major changes in nutrient supply to Welcome and Wavy lakes over the 10-yr period of observation were not measured and

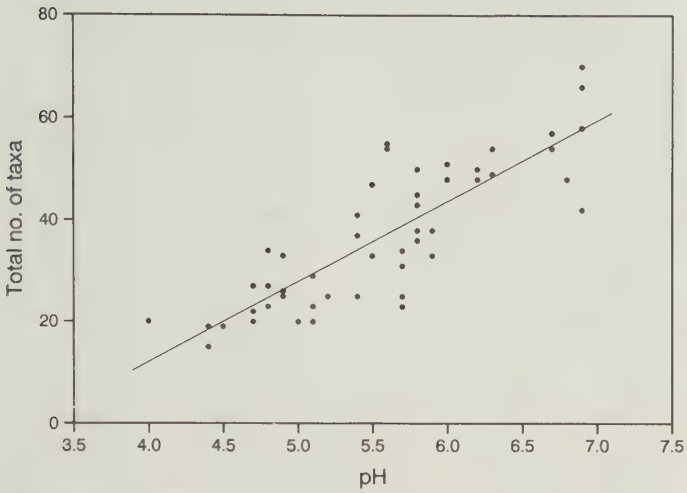

FIG. 11. Relationship between lake pH and total number of phytoplankton taxa in the seven Sudbury area lakes ($r^2 = 0.731$, $n = 52$).

therefore cannot be inferred as the reason for phytoplankton biomass changes in these lakes. Trophic state may have been influenced by changes in grazing pressure from secondary producers which may have been influenced by changes in fish community structure or other environmental variables. The observed species richness increase in Welcome Lake has been tentatively explained on the basis of a total biovolume – species richness relationship. However, it is likely that metal concentrations declined (even though acidity did not change measurably) over the past decade because Welcome Lake is within a geographic zone influenced by metal contributions from the Sudbury smelter (Keller and Pitblado 1986). For example, limited data suggest that surface water concentrations of copper declined from about 3 to 1 μg/L between the mid-1970's and the mid-1980's (Keller and Yan 1991). Some of the increase in taxonomic richness in Welcome Lake may therefore have resulted from decreased metal stress. In Joe Lake, 77% of all taxonomic shifts in abundance were predictable on the basis of the CANOCO ordinations (the aluminum axis and the alkalinity/trophic status axes). But, becauase there was no evidence of a major change in trophic state (total phytoplankton biomass actually decreased slightly between the mid-1970's and the mid-1980's), the increase in phytoplankton species richness was most probably a direct response to the increase in pH from 5.6 to 6.3.

Damage to phytoplankton communities in acidified lakes through loss of species richness would appear to be reversible. These findings, together with the documented recoveries of other biotic groups in Sudbury area lakes (Keller et al. 1992), demonstrate that SO_2 emission controls and associated decreased acid deposition to lakes may lead eventually to restoration of aquatic communities, given adequate opportunities for dispersal and recolonization by aquatic organisms.

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References

ALMER, B., W. DICKSON, E. EKSTRÖM, E. HÖRNSTRÖM, and U. MILLER. 1974. Effects of acidification on Swedish lakes. Ambio 3: 30–36.

DILLON, P. J., R. A. REID, AND R. GIRARD. 1986. Changes in the chemistry of lakes near Sudbury, Ontario following reductions of SO_2 emissions. Water Air Soil Pollut. 31: 59–66.

DILLON, P. J., N. D. YAN, W. A. SCHEIDER, AND N. CONROY. 1979. Acidic lakes in Ontario: characterization, extent, and responses to base and nutrient additions. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 317–336.

DIXIT, S. S., A. S. DIXIT, AND J. P. SMOL. 1989. Relationships between chrysophyte assemblages and environmental variables in seventy-two Sudbury lakes as examined by canonical correspondence analysis (CCA). Can. J. Fish. Aquat. Sci. 46: 1667–1676.

EARLE, J. C., H. C. DUTHIE, AND D. A. SCRUTON. 1986. Analysis of the phytoplankton composition of 95 Labrador lakes, with special reference to natural and anthropogenic acidification. Can. J. Fish. Aquat. Sci. 43: 1804–1811.

1987. Factors influencing the distribution of phytoplankton in 97 headwater lakes in insular Newfoundland. Can. J. Fish. Aquat. Sci. 44: 639–649.

ERIKSSON, F., E. HÖRNSTRÖM, P. MOSSBERG, AND P. NYBERG. 1983. Ecological effects of lime treatment of acidified lakes and rivers in Sweden. Hydrobiologia 101: 145–164.

FANGSTRÖM, I., AND E. WILLÉN. 1987. Clustering and canonical correspondence analysis of phytoplankton and environmental variables in Swedish lakes. Vegetatio 71: 87–95.

FINDLAY, D. L., AND S. KASIAN. 1990. Phytoplankton communities of lakes experimentally acidified with sulfuric and nitric acids. Can. J. Fish. Aquat. Sci. 47: 1378–1386.

GEELEN, J., AND R. LEUVEN. 1986. Impact of acidification on phytoplankton and zooplankton communities. Experientia 42: 486–494.

HAVENS, K. E., AND J. DECOSTA. 1984. The effects of acidification and phosphorus addition on phytoplankton biomass and productivity in a circumneutral mesotrophic lake receiving acid precipitation. Arch. Hydrobiol. Suppl. 69 (Monogr. Beiträge) 4: 443–476.

1987. The role of aluminum contamination in determining phytoplankton and zooplankton responses to acidification. Water Air Soil Pollut. 33: 277–293.

HÖRNSTRÖM, E., AND C. EKSTRÖM. 1986. Acidification and liming effects on phyto- and zooplankton in some Swedish West Coast lakes. Statens Naturvårdsverk. Rapp. 1864: 1–108.

HUTCHINSON, T. C., AND M. HAVAS. 1986. Recovery of previously acidified lakes near Coniston, Canada following reductions in atmospheric sulphur and metal emissions. Water Air Soil Pollut. 28: 319–333.

KELLER, W., J. M. GUNN, AND N. D. YAN. 1992. Evidence of biological recovery of acid stressed lakes near Sudbury, Canada. Environ. Pollut. 78: 79–85.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

KELLER, W., AND N. D. YAN. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

KEREKES, J. J., A. C. BLOUIN, AND S. T. BEAUCHAMP. 1990. Trophic responses to phosphorus in acidic and non-acidic lakes in Nova Scotia, Canada. Hydrobiologia 191: 105–110.

KWIATKOWSKI, R. E., AND J. C. ROFF. 1976. Effects of acidity on the phytoplankton and primary productivity of selected northern Ontario lakes. Can. J. Bot. 54: 2546–2561.

MACISAAC, H. J., W. KELLER, T. C. HUTCHINSON, AND N. D. YAN. 1986. Natural changes in the planktonic Rotifera of a small acid lake near Sudbury, Ontario following water quality improvements. Water Air Soil Pollut. 31: 791–797.

MCCAULEY, E., AND F. BRIAND. 1979. Zooplankton grazing and phytoplankton richness: field tests of the predation hypothesis. Limnol. Oceanogr. 24: 243–252.

MINNS, C. K., J. E. MOORE, D. W. SCHINDLER, AND M. L. JONES. 1990. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. III. Predicting impacts on species richness in seven groups of aquatic biota. Can. J. Fish. Aquat. Sci. 47: 821–830.

MOLOT, L. A., L. HEINTSCH, AND K. H. NICHOLLS. 1990. Response of phytoplankton in acidic lakes in Ontario to whole-lake neutralization. Can. J. Fish. Aquat. Sci. 47: 422–431.

MORLING, G., AND T. WILLÉN. 1990. Acidification and phytoplankton development in some west-Swedish lakes 1966–1983. Limnologica (Berl.) 20: 291–306.

NICHOLLS, K. H., AND E. C. CARNEY. 1979. The taxonomy of Bay of Quinte phytoplankton and the relative importance of common and rare taxa. Can. J. Bot. 57: 1591–1608.

PAUL, B. J., AND C. NALEWAJKO. 1984. pH–aluminum effects on phytoplankton. Verh. Int. Ver. Limnol. 22: 281. (Abstr.)

PILLSBURY, R. W., AND J. C. KINGSTON. 1990. The pH-independent effect of aluminum on cultures of phytoplankton from an acidic Wisconsin lake. Hydrobiologia 194: 225–233.

PINEL-ALLOUL, B., B. METHOT, G. VERRAULT, AND Y. VIGNEAULT. 1990. Phytoplankton in Quebec lakes: variation with lake morphometry, and with natural and anthropogenic acidification. Can. J. Fish. Aquat. Sci. 47: 1047–1057.

PITBLADO, J. R., AND W. KELLER. 1984. Data report — Monitoring of northeastern Ontario lakes 1981–1983. Ontario Ministry of the Environment, NE Region, Sudbury, Ont.

RADDUM, G., A. HOBAEK, E. LOMSLAND, AND T. JOHNSEN. 1980. Phytoplankton and zooplankton in acidified lakes in South Norway, p. 332–333. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980. SNSF Project, Oslo-Aas, Norway.

SIVER, P. A., AND J. S. HAMER. 1990. Use of extant populations of scaled chrysophytes for the inference of lake water pH. Can. J. Fish. Aquat. Sci. 47: 1339–1347.

STOKES, P. M. 1986. Ecological effects of acidification on primary producers in aquatic systems. Water Air Soil Pollut. 30: 421–438.

TER BRAAK, C. 1988. CANOCO — a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agr. Math. Group. Tech. Rep. LWA-88-02, Wageningen, The Netherlands.

TER BRAAK, C., AND H. VAN DAM. 1989. Inferring pH from diatoms: a comparison of old and new calibration methods. Hydrobiologia 178: 209–223.

WEATHERLEY, N. S. 1988. Liming to mitigate acidification in freshwater ecosystems: a review of the biological consequences. Water Air Soil Pollut. 39: 421–437.

WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, IL.

WILLIAMS, T. G., AND D. H. TURPIN. 1987. Photosynthetic kinetics determine the outcome of competition for dissolved inorganic carbon by freshwater microalgae: implications for acidified lakes. Oecologia (Berl.) 73: 307–311.

WILLÉN, E., S. HAJDU, AND Y. PEJLER. 1990. Summer phytoplankton in 73 nutrient-poor Swedish lakes. Classification, ordination and choice of long-term monitoring objects. Limnologica (Berl.) 20: 217–227.

YAN, N. D. 1979. Phytoplankton community of an acidified heavy metal-contaminated lake near Sudbury, Ontario: 1973–1977. Water Air Soil Pollut. 11: 43–55.

YAN, N. D., AND P. J. DILLON. 1984. Experimental neutralization of lakes near Sudbury, Ontario, p. 417–456. *In* J. Nriagu, [ed.] Environmental impacts of smelters. John Wiley & Sons Inc., New York, NY.

YAN, N. D., AND G. E. MILLER. 1984. Effects of deposition of acids and metals on chemistry and biology of lakes near Sudbury, Ontario, p. 244–282. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley & Sons Inc., New York, NY.

Appendices

APPENDIX 1. List of lakes and locations sampled for phytoplankton. The numbers correspond to those used in Fig. 4d, 5, and 7.

Lake No.	Lake name	Latitude	Longitude
2	Windy	46°36′W	81°27′W
6	Skill	46°27′N	81°24′W
16	Raft	46°24′N	80°57′W
17	McFarlane	46°25′N	80°59′W
37	Kakakiwaganda	46°11′N	80°47′W
38	Magnetawan R.	45°44′N	80°23′W
39	Naiscoot	45°31′N	80°20′W
40	Round	45°31′N	80°08′W
41	Otter	45°17′N	79°58′W
42	Trout	45°32′N	80°10′W
45	Eagle	45°50′N	79°30′W
47	Shawanaga	45°34′N	79°59′W
50	Chiniguchi	46°57′N	80°42′W
54	Laura	46°53′N	80°38′W
56	Temagami	47°10′N	80°08′W
60	Lady Evelyn	47°20′N	80°10′W
65	Hammond	47°31′N	79°52′W
67	Yorston	47°03′N	80°32′W
68	Bassoon	46°13′N	81°23′W
69	Bear	46°12′N	81°27′W
70	Threenarrows	46°05′N	81°27′W
71	Nellie	46°07′N	81°30′W
72	Elizabeth	46°15′N	81°38′W
75	Helen	46°07′N	81°34′W
77	Annie	46°11′N	81°08′W
79	O.S.A.	46°03′N	81°24′W
80	George	46°02′N	81°24′W
83	Margaret	46°17′N	81°27′W
86	Shoofly	47°13′N	81°24′W
87	Barnet	47°10′N	81°11′W
88	Welcome	47°13′N	81°02′W
92	Sunnywater	47°24′N	80°37′W
93	Laundrie	47°07′N	80°52′W
94	Florence	47°15′N	80°33′W
95	Mountain	47°39′N	80°14′W
101	Armstrong	46°32′N	81°33′W
113	Tyson	46°07′N	81°07′W
114	Bell	46°08′N	81°12′W
115	Bird	46°04′N	80°56′W
116	Broker	46°08′N	81°00′W
117	Fraleck	46°55′N	80°53′W
118	Telfer	46°56′N	80°47′W
123	Frederick	47°02′N	80°44′W
125	Obushkong	47°42′N	80°48′W
126	Shack	47°30′N	80°37′W
127	Makobe	47°27′N	80°27′W
128	McKee	47°23′N	80°55′W
129	Solace	47°11′N	80°42′W
130	Alphretta	46°59′N	80°46′W
131	Sam Martin	46°53′N	80°48′W
132	Hutton	46°49′N	81°00′W
133	Morrison	44°52′N	79°27′W
134	Bigwind	45°03′N	79°03′W
136	Nine Mile	44°57′N	79°35′W
137	Skeleton	45°15′N	79°27′W
138	Bass	45°06′N	79°42′W
139	Blackwater	45°25′N	79°49′W
140	Horn	45°24′N	79°36′W
143	Klock	47°28′N	80°08′W
144	Wawashkesh	45°43′N	80°02′W
145	Lahay	47°06′N	80°23′W
147	Erables	46°00′N	78°48′W
148	Biggar	45°57′N	78°55′W
149	La Muir	45°50′N	78°35′W
150	Proulx	45°46′N	78°24′W
152	Chateau	46°06′N	78°01′W
153	Foys	45°47′N	77°53′W
154	Brûle	45°38′N	78°49′W
155	Buck	45°25′N	79°23′W
156	Tim	45°45′N	79°02′W
157	Bernard	45°45′N	79°23′W
159	Red Pine	45°12′N	78°42′W
160	Smoke	45°31′N	78°41′W
161	Louisa	45°28′N	78°29′W
162	Hunter	46°21′N	81°48′W
173	Shining Tree	47°33′N	81°04′W
175	Little Burwash	47°06′N	81°07′W
177	Mary	45°15′N	79°15′W
181	Whitepine	47°23′N	80°38′W
185	Chief	47°29′N	80°06′W
186	Lady Sydney	47°24′N	80°12′W
187	Trethewey	47°26′N	80°30′W
188	Sugar	47°21′N	80°06′W
190	Banks	47°30′N	80°20′W
193	Lepha	47°32′N	80°03′W
195	Anvil	47°25′N	80°16′W
196	Mendelssohn	47°32′N	80°12′W

197	Wabun	47°25′N	80°36′W	224	Killarney	46°04′N	81°22′W
198	Anima Nipissing	47°14′N	79°57′W	225	Bowland	47°05′N	80°50′W
200	Cooke	47°36′N	80°21′W	236	Bluesucker	47°10′N	80°37′W
203	Mowat	46°52′N	80°57′W	237	Dougherty	47°01′N	80°40′W
204	Kasakanta	47°27′N	81°09′W	239	Carlyle	46°04′N	81°17′W
206	Lang	46°10′N	81°40′W	241	Linger	47°05′N	80°30′W
207	Halifax	46°14′N	81°01′W	242	Little Laundrie	47°07′N	80°47′W
209	Burwash	47°07′N	81°03′W	244	Seagram	47°06′N	80°32′W
211	Manitouwabing	45°29′N	79°54′W	246	Parkin	46°53′N	80°52′W
214	David	46°08′N	81°18′W	249	Pilgrim	47°11′N	80°41′W
215	Johnnie	46°07′N	81°14′W	250	Rome	47°00′N	81°19′W
219	Mahzenazing	46°03′N	81°11′W				

APPENDIX 2. List of taxa identified in summer phytoplankton samples. The numbers correspond to those used in Fig. 6.

1	*Anabaena*	62	*Ankistrodesmus*
2	*Aphanizomenon*	63	*Arthrodesmus*
3	*Aphanocapsa*	64	*Bambusina*
4	*Aphanothece*	65	*Botryococcus*
5	*Chroococcus*	66	*Carteria*
6	*Coelosphaerium*	67	*Chlamydomonas*
7	*Gomphosphaeria*	68	*Chodatella*
8	*Lyngbya*	69	*Closterium*
9	*Merismopedia*	70	*Coelastrum*
10	*Microcystis*	71	*Cosmarium*
11	*Oscillatoria*	72	*Crucigenia*
12	*Rhabdoderma*	73	*Dictyosphaerium*
13	*Ceratium*	74	*Elakatothrix*
14	*Gymnodinium*	75	*Euastrum*
15	*Peridinium*	76	*Eudorina*
16	*Peridinium inconspicuum*	77	*Franceia*
17	*Peridinium limbatum*	78	*Gloeocystis*
18	*Peridinium wisconsinense*	79	*Kirchneriella*
19	*Urococcus*	80	*Micrasterias*
20	Unidentified armoured dinophyceae	81	*Monoraphidium*
21	Unidentified dinophyceae	82	*Mougeotia*
22	Unidentified naked dinophyceae	83	*Nephrocytium*
23	*Bicosoeca*	84	*Oedogonium*
24	*Bitrichia*	85	*Oocystis*
25	*Chromulina*	86	*Paramastix*
26	*Chromulina erkensis*	87	*Pediastrum*
27	*Chrysochromulina*	88	*Pedinomonas*
28	*Chrysochromulina breviturrita*	89	*Planctonema*
29	*Chrysochromulina parva*	90	*Quadrigula*
30	*Chrysococcus*	91	*Scenedesmus*
31	*Chrysolykos*	92	*Schroederia*
32	*Chrysolykos* cysts	93	*Spondylosium*
33	*Chrysolykos planctonicus*	94	*Staurastrum*
34	*Chrysolykos skujai*	95	*Staurodesmus*
35	*Chrysosphaerella*	96	*Teilingia*
36	*Chrysosphaerella coronacircumspina*	97	*Tetraëdron*
37	*Chrysosphaerella longispina*	98	*Tetrastrum*
38	*Dinobryon*	99	*Ulothrix*
39	*Dinobryon* cysts	100	*Xanthidium*
40	*Kephyrion*	101	Unidentified chlorophyceae
41	*Mallomonas*	102	Unidentified chlorophycean cysts
42	*Mallomonas a*	103	*Achnanthes*
43	*Mallomonas b*	104	*Asterionella*
44	*Ochromonas*	105	*Cyclotella*
45	*Salpingoeca*	106	*Cymbella*
46	*Spiniferomonas*	107	*Eunotia*
47	*Synura*	108	*Fragilaria*
48	*Uroglena*	109	*Gomphonema*
49	*Uroglenopsis*	110	*Melosira*
50	Unidentified banana chrysophyte	111	*Navicula*
51	Unidentified chrysomonad	112	*Nitzschia*
52	Unidentified chrysophyte	113	*Rhizosolenia*
53	Unidentified chrysophycean cysts	114	*Rhizosolenia* chloroplasts
54	*Cryptomonas*	115	*Stauroneis*
55	*Cryptomonas a*	116	*Stephanodiscus*
56	*Cryptomonas b*	117	*Surirella*
57	*Katablepharis*	118	*Synedra*
58	*Rhodomonas*	119	*Tabellaria*
59	*Euglena*	120	*Tabellaria fenestrata*
60	*Phacus*	121	*Tabellaria flocculosa*
61	*Trachelomonas*		

Changes in Zooplankton during the Experimental Neutralization and Early Reacidification of Bowland Lake Near Sudbury, Ontario

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Keller, W., N. D. Yan, T. Howell, L. A. Molot, and W. D. Taylor. 1992. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 52–62.

The zooplankton of Bowland Lake was sampled before and for 6 yr after neutralization of the lake from pH 4.9 to 6.9. Changes in community composition, including decreased abundance of the acidophilic rotifers *Keratella taurocephala, Ploesoma lenticulare,* and *Gastropus stylifer* and increased abundance of *Keratella cochlearis, Polyarthra* sp., and other species, occurred after neutralization. Two crustacean species not previously seen in Bowland Lake, *Eubosmina tubicen* and *Epischura lacustris*, became important in the zooplankton in the second and fourth years, respectively, after neutralization. Subsequently, increases in the abundances of *K. taurocephala, G. stylifer,* and *P. lenticulare* and decreases in the abundance of *E. lacustris* occurred during the early reacidification of the lake, when average pH declined to approximately 5.5. Temporal patterns in the total abundances of crustaceans, rotifers, and ciliates appeared linked to biological interactions, including predation by fish and larval *Chaoborus*, not directly to water quality changes.

Des prélèvements de zooplancton ont été effectués dans le lac Bowland avant la neutralisation du lac du pH 4,6 au pH 6,9 et pendant les six années qui ont suivi. Après la neutralisation, on a assisté à des changements dans la composition des communautés, et notamment une diminution de l'abondance des rotifères acidophiles *Keratella taurocephala, Ploesoma lenticulare* et *Gastropus stylifer,* ainsi qu'une augmentation de l'abondance de *Keratella cochlearis, Polyarthra* sp. et d'autres espèces. Deux espèces de crustacés que l'on n'avait pas vues auparavant dans le lac Bowland, *Eubosmina tubicen* et *Epischura lacustris*, sont devenues importantes dans le zooplancton au cours respectivement des deuxième et quatrième années après la neutralisation. Par la suite, on a observé une augmentation de l'abondance de *K. taurocephala, G. stylifer* et *P. lenticulare* et une diminution de l'abondance de *E. lacustris* durant la réacidification précoce du lac, alors que le pH diminuait à environ 5,5. Les tendances temporelles de l'abondance totale des crustacés, des rotifères et des ciliés semblaient liées aux interactions biologiques, incluant la prédation par le poisson et par la larve de *Chaoborus* et ne semblaient pas directement reliées aux changements de la qualité de l'eau.

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Changes in zooplankton community structure associated with acidification, particularly losses of species leading to decreased community diversity, have been extensively documented (Almer et al. 1974; Sprules 1975; Roff and Kwiatkowski 1977; Brezonik et al. 1984; Keller and Pitblado 1984; Yan and Dillon 1984; Carter et al. 1986; MacIsaac et al. 1987; and others). Mechanisms responsible for changes in zooplankton communities have yet to be completely elucidated but appear to include changing interactions between trophic levels through changes in the abundance of predators or prey (Eriksson et al. 1980; Yan et al. 1982; Nilssen et al. 1984), altered competition (Yan and Geiling 1985), physical changes such as increased transparency (Yan 1983), or acid and metal toxicity (Brehm and Meijering 1982; Malley et al. 1982; Keller et al. 1990c).

The addition of neutralizing agents to reverse acidic conditions may allow acid-sensitive organisms to recolonize or lead to improvements in growth and reproduction in populations physiologically affected by acidification. However, reported effects of neutralization on zooplankton communities have varied, including no apparent influences (Yan et al. 1977; Nyberg 1984), positive responses (Hultberg and Andersson 1982; Nyberg 1984), and negative effects (Yan and Dillon 1984; Henrikson et al. 1985). Many factors probably contributed to

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TABLE 1. Average chemical characteristics for Bowland Lake, before and after neutralization.

	pH	Ca ($mg \cdot L^{-1}$)	Total Al ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)
1982 (n = 6–10)	5.2	2.87	128	6
1983[a] (n = 6–7)	4.9	2.72	139	—
1983[b] (n = 4–5)	6.9	4.41	80	4
1984 (n = 12–13)	6.5	4.46	47	5
1985 (n = 11)	6.3	3.81	50	5
1986 (n = 9–10)	6.1	3.72	39	4
1987 (n = 11)	6.3	3.18	28	4
1988 (n = 11)	5.7	3.19	39	6
1989 (n = 11)	5.5	2.95	60	4

[a]Before neutralization.
[b]After neutralization.

these different responses, including varying initial degrees of damage, the variable time scales of the studies (i.e. short-term versus long-term patterns), the availability of species for recolonization, and variation in the degree and rate of the actual chemical changes that resulted from specific neutralization activities. In addition, the biological attributes of lakes prior to manipulation, notably the presence and abundance of fish and invertebrate predators, may greatly affect changes in zooplankton communities that accompany neutralization (Nyberg 1984).

Given the variability in previous findings, the uncertainty over the controlling mechanisms, and the important role of zooplankton in energy transfer between trophic levels, studies of zooplankton communities in an acidic lake before and after neutralization were implemented under Ontario's Experimental Lake Neutralization Program. While several studies have examined the short-term chemical and biological effects of lake neutralization (e.g. Porcella 1989; Keller et al. 1990a), longer-term responses to neutralization are very poorly known. Our intent was to evaluate the qualitative and quantitative changes in the zooplankton community that accompanied neutralization and reintroduction of lake trout (*Salvelinus namaycush*) to Bowland Lake, a highly acidic (pH ~ 5.0) lake in which substantial biological damage had occurred. In particular, we assessed patterns of recolonization of acid-sensitive species and examined how changes in trophic interactions after neutralization were related to zooplankton community structure. Temporal patterns in the crustacean zooplankton community of the lake were assessed in comparison with data for a group of reference lakes in south-central Ontario. Comparable sets of reference data were not available for rotifers or ciliates; thus, evaluation of temporal patterns in rotifer and ciliate communities relied on comparisons with data from the literature.

Site Description

The neutralization of acidic Bowland Lake (47°05′N, 80°50′W) ~70 km north of Sudbury, Ontario (A_0 = 109 ha; $\bar{z}$ = 7.6 m), with 84 tonnes of powdered $CaCO_3$ in August 1983 is outlined in Molot et al. (1986). Water quality changes are described by Molot et al. (1990a) and are briefly summarized in Table 1. Gunn et al. (1990), Jackson et al. (1990), Keller et al. (1990b), and Molot et al. (1990b) described changes in the fish, littoral plant, zoobenthos, and phytoplankton assemblages, respectively.

Interannual changes in crustacean assemblages in Bowland Lake were compared with those observed between 1982 and 1988 in three intensively sampled nonacidified reference lakes in the district of Muskoka, ~200 km southeast of Bowland Lake. These lakes (Harp, Blue Chalk, Red Chalk) resemble Bowland Lake in terms of water clarity, ionic strength, nutrient status, and morphometry, but they have not acidified. Dillon et al. (1988) described the water quality and trophic status of these lakes; Yan and Strus (1980) and Yan (1986) described their zooplankton assemblages.

To determine if the crustacean assemblages in Bowland Lake responded to changes in pH in a manner characteristic of other lakes in Ontario, average community structure in each ice-free season between 1982 and 1989 was compared with that of one ice-free season of data available for 46 dimictic lakes chosen to vary widely in average pH (5.3–6.7). These lakes, selected to resemble Bowland Lake in general trophic status (total phosphorus (TP) < 15 $\mu g \cdot L^{-1}$), were located in the Haliburton, Parry Sound, Nipissing, and Muskoka districts of Ontario, southeast of Sudbury. The lakes varied in maximum depth (6.5–61 m), dissolved organic carbon (DOC) (1.4–5.8 $mg \cdot L^{-1}$), and TP (4–15 $\mu g \cdot L^{-1}$) (P. J. Dillon, unpubl. data). Raw data from these lakes are available from the second author on request.

Methods

Samples for ciliates were collected monthly from February 1983 to September 1989 at 2-m depth intervals from the central basin in Bowland Lake using a 3-L Van Dorn bottle and were preserved with Lugol's iodine (Taylor and Heynen 1987) in the field. Whole-lake volume-weighted samples were prepared by pooling aliquots of individual samples in proportion to the volumes of the strata from which they were obtained. Whole-lake volume-weighted samples of rotifers and crustacean zooplankton were also collected monthly at the same depth intervals as ciliate samples from June 1982 to September 1989 using a 30-L Plexiglas trap (Schindler 1969). The trap was fitted with 70-μm mesh in June and July 1982 and 55-μm mesh thereafter. No change in crustacean or rotifer abundance associated with the change in mesh size was observed. Animals were preserved in a 4% sucrose – 4% formalin solution. Whole-lake volume-weighted composite samples for enumeration were subsequently prepared.

About 300 crustaceans were examined except in samples with less than 300 individuals, when all crustaceans were identified. Copepodids were identified to suborder, while nauplii were simply enumerated. Rotifers were counted and identified in a Sedgewick–Rafter counting cell. Subsamples were examined until at least 300 organisms were identified. Ciliates were identified to genus where possible. Samples were settled and examined with an inverted phase-contrast microscope. At least 200 individuals were counted in a stratified design where a greater volume of water was searched for large species than for small species.

Crustacean samples from the reference lakes were collected on a monthly basis through the ice-free season as morphometrically weighted composites using tow nets equipped with 80-μm mesh. Sample collection, compositing, and enumeration methods are detailed in Girard and Reid (1990).

TABLE 2. Bowland Lake crustacean zooplankton taxa list, pre- and postneutralization. Species indicated by an asterisk were recorded on only one occasion.

Crustaceans	1982 (n = 10)	1983[a] (n = 6)	1983[b] (n = 3)	1984 (n = 11)	1985 (n = 10)	1986 (n = 10)	1987 (n = 9)	1988 (n = 9)	1989 (n = 8)
Cladocera									
Alona sp.	*								
Bosmina longirostris	P	P	P	P	P	P	P	P	P
Chydorus sphaericus	P	*	P	P	P		P	*	
Ceriodaphnia lacustris				*					
Daphnia ambigua						P			
Daphnia dubia						P			P
Daphnia g. mendotae	P			*	P		P	*	P
Daphnia pulex	P	P	P	P	P	P	P	P	P
Diaphanosoma birgei[c]				P		*		*	*
Diaphanosoma brachyurum	P	*		P	P				
Eubosmina longispina		*			*	*			
Eubosmina tubicen					P	P	P	P	P
Holopedium gibberum	P	P	P	P	P	P	P	P	P
Leptodora kindtii				*	*				*
Latona setifera			*					*	
Polyphemus pediculus	P					*			
Sida crystallina	*							*	
Calanoida									
Diaptomus minutus	P	P	P	P	P	P	P	P	P
Diaptomus oregonensis						*			
Epischura lacustris						P	P	P	P
Cyclopoida									
Cyclops bicuspidatus thomasi	P	P			P	P		P	P
Cyclops vernalis	*							*	
Mesocyclops edax	P	*	P	P	P	P	P	*	P
Orthocyclops modestus			*	P	P	P	*		
Tropocyclops prasinus mexicanus	P	P			P	P	P	P	P

[a]Preneutralization.
[b]Postneutralization.
[c]Classified as *D. brachyurum* before August 1983.

Nonmetric multidimensional scaling (NMDS; Kruskal 1964) ordination was used to compare patterns in average annual ice-free period crustacean species abundances for Bowland Lake and the south-central Ontario reference lakes. For NMDS ordinations, taxa encountered in only one lake were eliminated and the abundances of all taxa were log (x + 1) transformed, and a two-dimensional NMDS analysis was run using chord distance as the resemblance measure. Stress was acceptable at 20%. Correlations of limnological data with axis scores were examined, and probabilities were Bonferroni adjusted (Cooper 1968).

Results

We identified 25 crustacean species in plankton collections from Bowland Lake between June 1982 and September 1989 (Table 2). Only one species (*Alona* sp.) originally collected was not recorded in the plankton after neutralization, although it was initially very rare. Nine additional species were recorded after neutralization. Two of these new species, *Eubosmina tubicen* and *Epischura lacustris*, became common by 1985 and 1987, respectively; however, *E. lacustris* abundance declined again in 1989 (Fig. 1).

The planktonic crustacean community in Bowland Lake before neutralization was dominated by the calanoid copepod *Diaptomus minutus* and the cladocerans *Daphnia pulex* (Dodson 1981), *Bosmina longirostris*, and *Holopedium gibberum* (Fig. 1). The pattern of dominant species in the crustacean community was only slightly changed in the years after liming. *Diaptomus minutus*, *B. longirostris*, and *H. gibberum* continued to be generally abundant. *Diaptomus minutus* and *B. longirostris* gradually declined in abundance in the years following neutralization but increased to preneutralization abundances in the last two years of study (1988, 1989). After neutralization, a conspicuous short-term (1985) decrease in abundance, and then a later return to preneutralization abundances, was observed for *H. gibberum*. Total crustacean abundance followed an approximately similar pattern (Fig. 2). Average annual abundance for the ice-free period ranged from 8 to 36 animals·L^{-1}. Average abundance was highest in the two preneutralization years (1982, 1983) and in the last two years of study (1988, 1989) (Fig. 2, 3d).

Comparing temporal patterns in the Bowland Lake crustacean community with the reference lakes using NMDS indicated that the community remained clearly distinguishable from communities in nonacid lakes (Fig. 3a, 3b, 3c). An examination of first-axis NMDS scores plotted against pH (Fig. 3b) suggested that the Bowland Lake crustacean community was typical of acidic lakes in 1982 and 1983. The elevation of the lake's pH in 1984 and 1985 did not result in community structure characteristic of nonacidic lakes. However, by 1986 and 1987, the community was approaching that of nonacidic lakes. When the lake began to reacidify in 1988 and 1989, the community closely resembled that of survey lakes of similar pH. This pattern of changes was manifested as much higher interannual variation in community structure in Bowland Lake than in the three nonacidified reference lakes studied over the same 8-yr period (Fig. 3c).

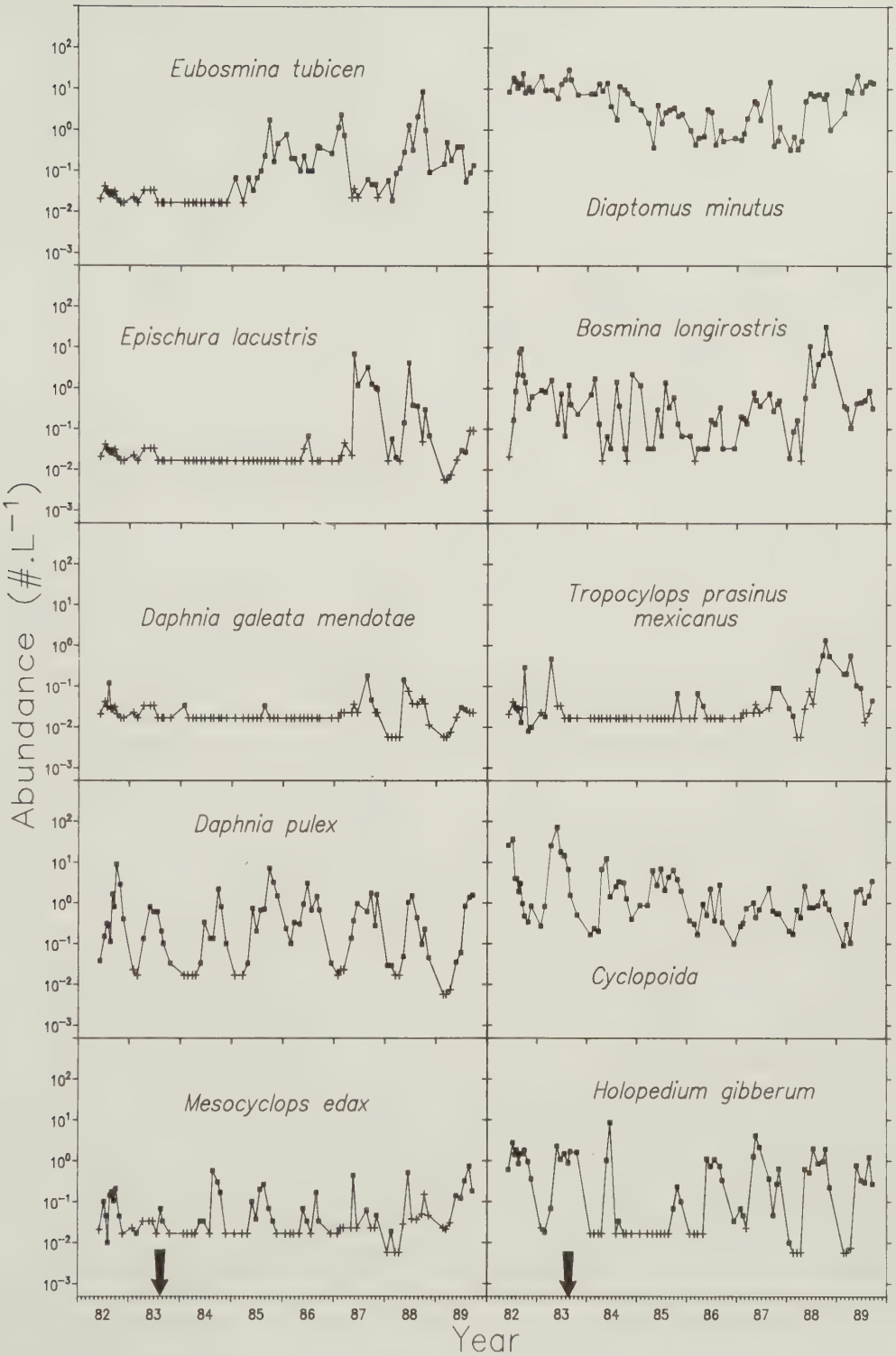

FIG. 1. Temporal patterns in the abundances of major crustacean zooplankton taxa in Bowland Lake, 1982–89. Arrows indicate neutralization date. When a taxon was not encountered in a sample, its abundance was reported as if one animal of that taxon was encountered in a volume equivalent to twice the largest subsample volume examined for any taxon in the composite sample on that date. These detection limit abundance estimates are represented with a plus sign.

First-axis NMDS scores (Fig. 3b) were positively correlated (Pearson's r) with pH ($r = 0.525$, $p = 0.001$), mean depth ($r = 0.446$, $p = 0.021$), and maximum depth ($r = 0.421$, $p = 0.043$) but not with DOC or TP. Second-axis scores were correlated with TP ($r = 0.429$, $p = 0.034$).

Of the 34 rotifer taxa collected in Bowland Lake during 1982–89, 18 were observed both before and after neutralization (Table 3). Five taxa were observed only prior to neutralization and 11 were observed only after neutralization, but these were generally not abundant.

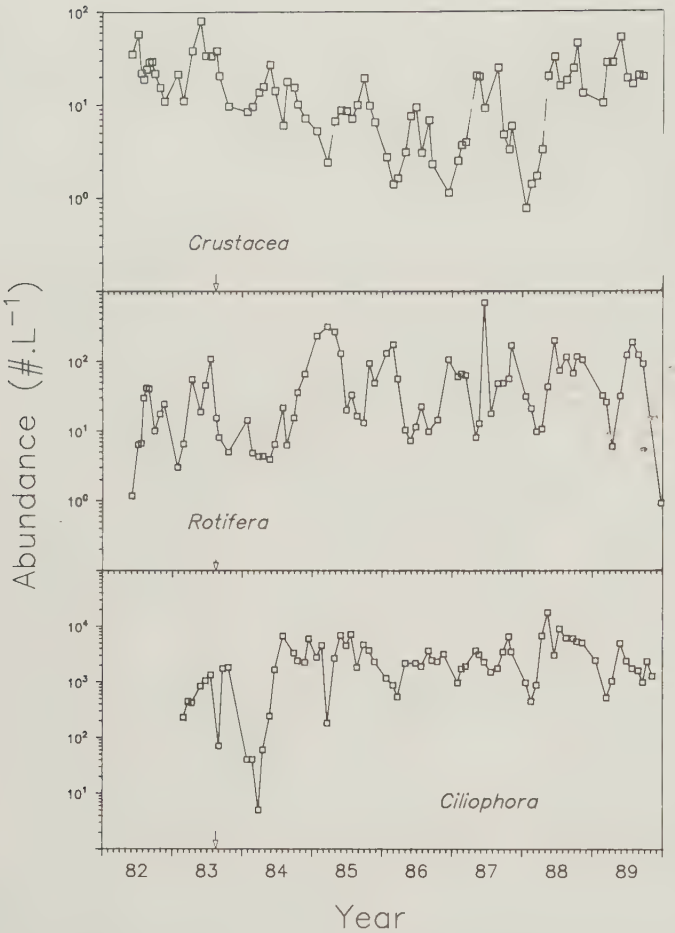

FIG. 2. Temporal patterns in the total abundance of crustacean, rotifer, and ciliate zooplankton in Bowland Lake, 1982–89. Arrows indicate neutralization date.

Rotifer abundance generally increased after neutralization, a change that persisted throughout the study (Fig. 2). Average annual rotifer abundance for the ice-free period ranged from 13 to 125 animals·L^{-1}. *Keratella taurocephala, Gastropus stylifer,* and *Ploesoma lenticulare* decreased in abundance for 3–4 yr after neutralization but returned to preneutralization abundances by the end of the study. *Keratella cochlearis, K. testudo, Kellicotia longispina, Conochilus unicornis,* and *Polyarthra* increased in abundance after neutralization (Fig. 4). Overall, dominance shifted dramatically from *K. taurocephala* to *K. cochlearis* after neutralization. Each of these species commonly contributed over 50% of the abundance during preneutralization and postneutralization periods, respectively.

Analysis of the data for ciliates (Table 4; Fig. 2) is greatly complicated by the brief preneutralization database (February–July 1983). The numerically dominant taxa in Bowland Lake were *Askenasia, Urotricha, Strombidium,* and *Strobilidium.* Average ciliate density during the annual ice-free period ranged from 1.1×10^3 to 4.3×10^3 animals·L^{-1}.

Discussion

The neutralization of acidic Bowland Lake did result in some colonization by acid-sensitive crustacean species; however, the lake did not return to a compositional structure typical of unimpacted lakes. While the composition of the crustacean community showed clear temporal changes, it did not achieve similarity with the communities of nonacidic reference lakes in south-central Ontario, indicating that despite some improvements, recovery related to neutralization was not complete in the four years when pH was >6.0.

The continuing numerical importance in the crustacean plankton community by *D. minutus* is typical of oligotrophic lakes in Ontario. While *D. minutus* is generally abundant and widespread in oligotrophic Ontario lakes (Patalas 1971; Hitchin and Yan 1983; Keller and Pitblado 1984), the relative imporance of the species increases in acidic lakes because of declines in more acid-sensitive species (Sprules 1975; Keller and Pitblado 1984). The absence of some common, apparently acid-sensitive (Sprules 1975; Keller and Pitblado 1984) species before neutralization, such as *E. lacustris, E. tubicen, Daphnia longiremis, Cyclops scutifer,* and *Diaptomus oregonensis*, is symptomatic of acid stress.

Recolonization of locally extirpated species can be expected to be very variable and may depend on colonization sources both internal and external to a lake (Carvalho and Wolf 1989; DeStasio 1989; Keller and Yan 1991). Recolonization rates for many crustacean species are generally in the order of 1 yr or longer (Von Ende and Dempsey 1981; Fryer 1985; Keller and Yan 1991), and it is also possible that temporarily high planktivore (yellow perch (*Perca flavescens*) and *Chaoborus*) populations in Bowland Lake (Gunn et al. 1990; Keller et al. 1990b) may have retarded the establishment of new species by keeping population levels low after neutralization (Von Ende and Dempsey 1981). However, the appearance of species previously absent, particularly *E. lacustris* (1986–89) and *E. tubicen* (1985–89), indicates that some recolonization by acid-sensitive crustacean species had occurred. Reestablishment of species may, however, be short lived if lakes reacidify. In Bowland Lake, *E. lacustris* showed evidence of a decline early during reacidification of the lake, when average annual pH dropped to ~5.5. This observation is consistent with the documented disappearance of *E. lacustris* at pH ~5.6 from experimentally acidified Lake 223, Ontario (Schindler et al. 1985).

The abundance of crustacean zooplankton in Bowland Lake (annual ice-free period averages 8–36 animals·L^{-1}) was similar to values reported for seven near-neutral oligotrophic lakes in south-central Ontario (18–46 animals·L^{-1}; Yan and Strus 1980), and it is unlikely that the apparent postneutralization decrease in abundance, which extended over a period of 2–3 yr (Fig. 2), was a manifestation of direct chemical effects. Declines in the abundances of *B. longirostris* and *D. minutus* (Fig. 1), species not considered acid sensitive, were major components of the observed decrease in total crustacean abundance (Fig. 2).

Short-term decreases in crustacean zooplankton abundance, probably attributable to pH shock, have been reported in other neutralization studies (Yan and Dillon 1984); however, the degree of pH alteration was much greater than in the present experiment. Less extreme manipulation of lake pH did not decrease crustacean biomass in Nelson Lake, Ontario (Yan et al. 1977). It is more likely that the observed postneutralization declines in crustacean abundance in Bowland Lake were related to large transient increases in fish (Gunn et al. 1990) and *Chaoborus* (Fig. 3e) populations which could not be directly attributed to lake neutralization.

Temporal patterns in crustacean abundance during this study generally followed patterns observed during the same period in two of the three morphometrically similar, near-neutral reference lakes in south-central Ontario (Harp and Blue Chalk). However, between-year variations were much greater in Bow-

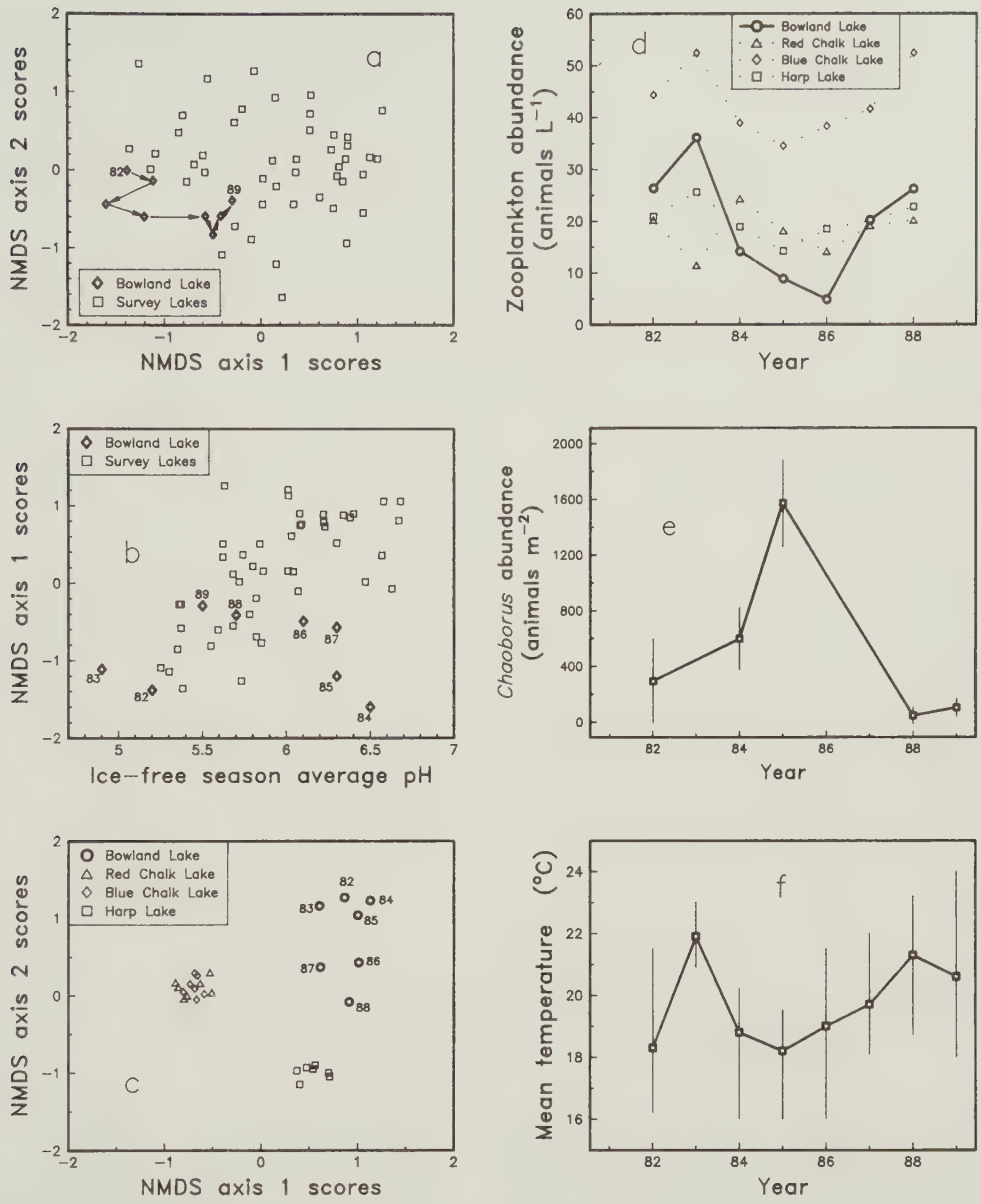

FIG. 3. Summary of comparisons of crustacean zooplankton data from Bowland Lake and the reference lakes. (a) Two-dimensional ordination of ice-free season average community structure of Bowland Lake and the 46 reference lakes; (b) scattergram of axis 1 scores from Fig. 3a with the best environmental correlate, lake water pH; (c) two-dimensional ordination of ice-free season average community composition for 1982–88 from Bowland Lake and the three nonacidified, long-term reference lakes; (d) comparison of temporal changes in average abundance of all crustacean zooplankton in these four lakes; (e) average abundance of *C. punctipennis* in hypolimnetic sediment core samples from Bowland Lake (error bars represent 2 standard errors; grand mean and standard errors were derived from eight station means); (f) average annual summer (June 1 to September 15) water temperatures at 2 m depth in Bowland Lake (vertical bars give the minimum and maximum temperatures recorded during the period).

land Lake (Fig. 3d). This suggests that the temporal variations observed in Bowland Lake are the result of lake-specific influences such as fish and *Chaoborus* predation superimposed on broad, generalized changes in abundance related to factors such as regional weather fluctuations.

Short-term postneutralization decreases in the abundance of crustacean zooplankton, particularly the large *H. gibberum*, probably were related to intense predation by the very abundant 1983 year class of yellow perch (Gunn et al. 1990), which initially would rely heavily on small prey including microcrustaceans (Keast 1977; Chabot and Maly 1986). *Holopedium*, in particular, may be an important prey for yellow perch (Arts and Sprules 1989). Predation on crustacean zooplankton by introduced lake trout also occurred, as indicated by the presence of zooplankton, notably *Daphnia*, in trout stomachs (Gunn et al. 1990). A large decrease in the abundance of crustacean zooplankton in Lake Stensjon, Norway, after neutralization was attributed to increased predation, which, in turn, was related to improved survival of young-of-the-year perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) (Henrikson et al. 1985).

With a 10-fold increase in the abundance of *Chaoborus punctipennis* in 1985 (Fig. 3e; Keller et al. 1990b), *Chaoborus* pre-

TABLE 3. Bowland Lake rotifer taxa list, pre- and postneutralization. Species indicated by an asterisk were recorded on only one occasion.

Rotifers	1982 (n = 9)	1983[a] (n = 6)	1983[b] (n = 3)	1984 (n = 11)	1985 (n = 10)	1986 (n = 10)	1987 (n = 10)	1988 (n = 9)	1989 (n = 8)
Ascomorpha ovalis				P		P	*		*
Asplanchna priodonta	P		P	P	P		*		*
Cephalodella						*			
Collotheca							P	*	P
Collotheca mutabilis	P								
Conochilus unicornis	P	*	*	P	P	P	P	P	P
Conochilus hippocrepis							*		
Conochiloides	*	*				*			
Filinia terminalis			P	P			*		
Euchlanis						*			
Gastropus hyptopus				*		*			
Gastropus stylifer	P	P	P	P			*		P
Kellicottia longispina	*	P	P	P	P	P	P	P	P
Kellicottia bostoniensis	P	P	P	P	P	P	P	P	P
Keratella crassa	P	P	P	P	P	P	P	P	P
Keratella cochlearis	P	P	P	P	P	P	P	P	P
Keratella hiemalis	*			P		P			P
Keratella quadrata					*		*		
Keratella taurocephala	P	P	P	P	P	P	P	P	P
Keratella testudo				P	P	P	P	P	P
Keratella serrulata						*		P	
Lecane	P	*		P	P				*
Lepadella acuminata	*								
Monostyla	P	P	*	*			P		
Monommata	*								
Ploesoma lenticulare	P	P	P	P		P	*	P	P
Polyarthra	P	P	P	P	P	P	*	P	P
Synchaeta	P	P	P	P	P	P	P	P	P
Testudinella	*	*							
Trichocerca cylindrica	P	*	*	*				*	
Trichocerca multicrinis	P		*	*			*		
Trichocerca porcellus					P				
Trichocerca rousseleti	*	*							
Trichocerca similis	P					P			

[a]Preneutralization.
[b]Postneutralization.

dation probably became a factor affecting crustacean plankton abundance. Substantial declines in the population of *D. minutus* in 1985 (Fig. 1), a species not apparently favoured as prey by yellow perch (Chabot and Maly 1986), suggest an influence by *Chaoborus* predation in Bowland Lake. Numerous studies have demonstrated that *Chaoborus* can decimate crustacean zooplankton prey populations (Lynch 1979; Yan et al. 1982; Nyberg 1984). The very high *Chaoborus* abundance in Bowland Lake in 1985 ($1534 \cdot m^{-2}$) greatly exceeded the mean ($226 \cdot m^{-2}$) and maximum ($1198 \cdot m^{-2}$) abundances of *C. punctipennis* observed in 55 south-central Ontario lakes ranging widely in pH (4.8–6.7), TP (4–45 $\mu g \cdot L^{-1}$), and mean depth (2.7–20.5 m) (N. D. Yan, unpubl. data).

The observation that crustacean zooplankton abundance had returned to preneutralization levels by 1989 (Fig. 2) supports the predation hypothesis because in the latter years of study the *C. punctipennis* population had returned to very low levels (Fig. 3e) and new perch year classes were much reduced in comparison with the 1983 year class (Experimental Neutralization Study, unpubl. data). Temperature may also be an additional factor which influenced zooplankton abundance because three of the years with the highest crustacean abundance (1983, 1988, 1989) also had the warmest summer water temperatures (Fig. 3f).

The rotifer *K. taurocephala* commonly dominates rotifer communities in acidic lakes in North America (Roff and Kwiatkowski 1977; Bradt et al. 1984; Siegfried et al. 1984; Yan and Geiling 1985; MacIsaac et al. 1987). Dramatic declines in the importance of *K. taurocephala* commence at about pH 4.8 (MacIsaac et al. 1987) and the species is virtually absent from circumneutral lakes. The replacement of *K. taurocephala* by *K. cochlearis, Polyarthra* sp., and other species after the neutralization of Bowland Lake (Fig. 4), while clearly linked to reduced acidity and consistent with results from other neutralization experiments (Schaffner 1989), may, however, partially reflect altered biotic interactions and not direct water quality effects. For example, while *K. cochlearis* clearly declines in acidic lakes, laboratory experiments have demonstrated that this species is actually acid tolerant (Havens and DeCosta 1988). Susceptibility to predation may be an important factor in lakes such as Bowland, with at least periodically abundant *Chaoborus*. Characteristics such as body spines or rapid escape tactics can lead to selective predation on zooplankton by *Chaoborus* (Moore and Gilbert 1987; Havens 1990).

Keratella cochlearis and *Polyarthra* are common dominants in near-neutral Sudbury area lakes (Roff and Kwiatkowski 1977; MacIsaac et al. 1987), and *Polyarthra* has previously been shown to assume increasing importance with declines in lake acidity and decreases in *K. taurocephala* abundance (MacIsaac et al. 1986). The increases in abundance observed for *K. taurocephala, G. stylifer,* and *P. lenticulare* near the end of the study period probably reflect the early reacidification of

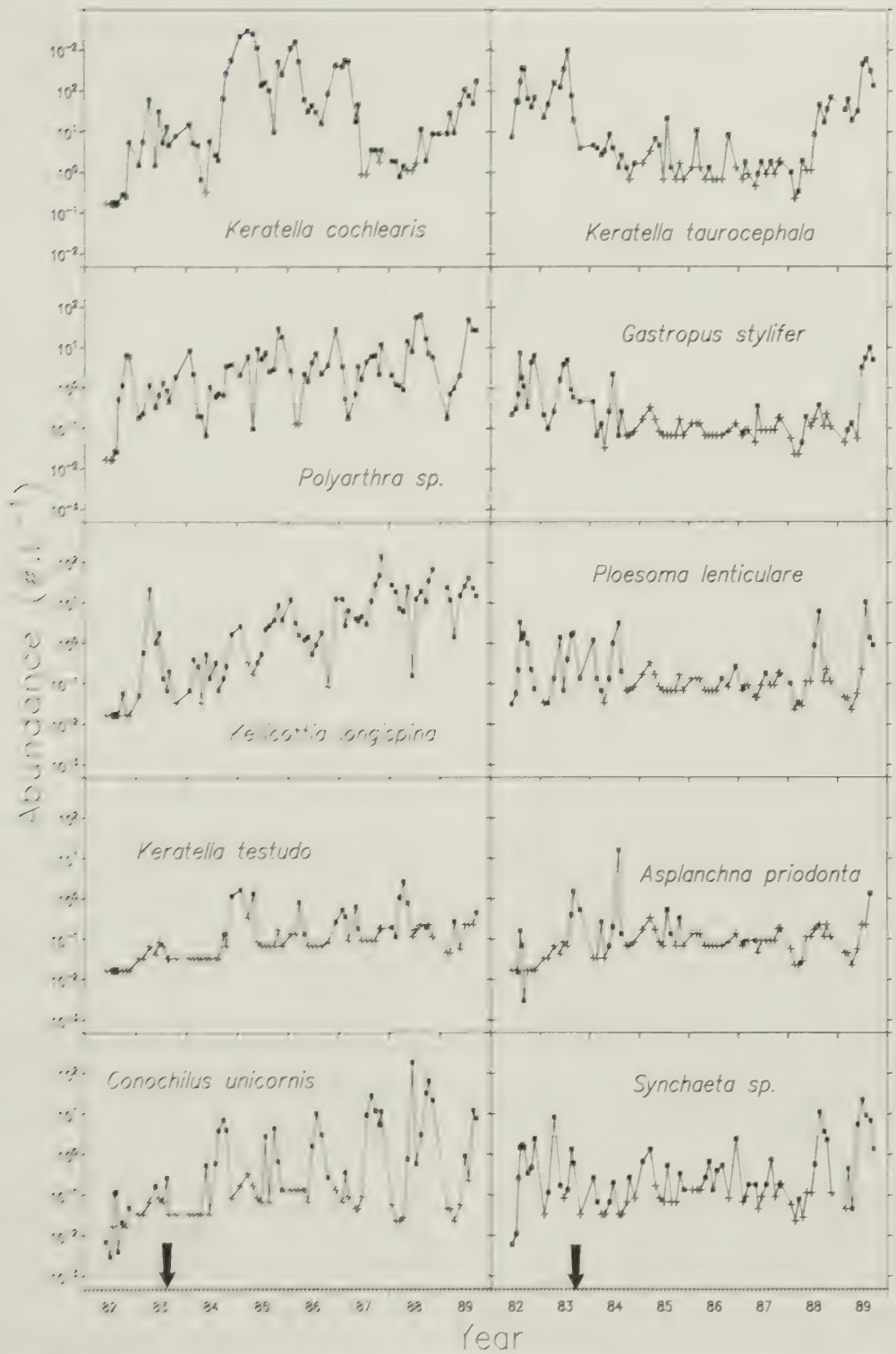

FIG. 4. Temporal patterns in the abundances of major rotifer taxa in Bowland Lake, 1982–89. Arrows indicate neutralization date. Zero values were adjusted as outlined in Fig. 1.

the lake; however, it is noteworthy that rotifers that are normally negatively associated with acid conditions, such as *K. cochlearis*, *Polyarthra*, and *K. longispina*, did not show evidence of a decline (Fig. 4).

Temporal patterns in Bowland Lake suggest that reduced crustacean densities allowed substantial increases in rotifer and ciliate abundance, possibly through competitive release. Yan and Geiling (1985) attributed elevated rotifer biomass and abundance in two acidified lakes in Ontario to reduced competition from herbivorous crustaceans. Postneutralization increases in rotifer abundance in Bowland Lake corresponded closely with declines in crustacean abundance, notably *H. gibberum*, which, with the exception of one short peak of high abundance, maintained reduced populations during 1984 and 1985. Such increases in rotifer abundance associated with declines in populations of larger grazers have been frequently reported (e.g. Andersson et al. 1978; Neill 1984; Cryer et al. 1986; Threlkeld and Choinski 1987) and are a common consequence of fish

TABLE 4. Major ciliate taxa in Bowland Lake, pre- and postneutralization. Taxa indicated by an asterisk were recorded on only one occasion.

Class/taxon	1983[a] (n = 6)	1983[b] (n = 3)	1984 (n = 11)	1985 (n = 11)	1986 (n = 8)	1987 (n = 10)	1988 (n = 8)	1989 (n = 9)
Spirotrichea								
Tintinnidium	*				*			
Strobilidium velox	P	P	P	P	P	P	P	P
Strobilidum spp.	P	P	P	P	P	P	P	P
Halteria		*	P	P	P	P	*	*
Strombidium	P	P	P	P	P	*	P	P
Stichotricha					P		*	*
Prostomatea								
cf. *Hololphrya*			*	*	*	P	*	*
cf. *Balanion*	P	*	P	P	P	P	*	P
Coleps		P	*	P	*			*
Urotricha pelagica	*		P	P	P	P	P	P
Urotricha spp.	P	*	P	P	P	P	P	P
Litostomtea								
Askenasia	P	*	P	P	P	P	P	P
Mesodinium			P	P	P	P	P	P
Lagynophrya	*				P	P	P	
Nassophorea								
Stokesia					P	P		P
Oligohymenophorea								
Cyclidium		*	P	P	P	P	P	P
Scuticociliate			P	P	P	P	P	P
Campanella	P				*	P	*	P
Vorticella			P	P	P	P	P	P

[a]Preneutralization.
[b]Postneutralization.

predation on large zooplankton (Hurlbert and Mulla 1981; Gilbert 1988). Improved food resources may also be a factor in the expansion of rotifer populations, since after neutralization the phytoplankton community shifted from blue-greens to chrysophytes and tended to increase in biovolume (Molot et al. 1990b). This may also explain the observation that rotifer abundance remained high at the end of the study, even though crustacean abundance had returned to preneutralization levels. Average annual ice-free period rotifer abundances (13–125 animals·L^{-1}) were comparable with values (28–184 animals·L^{-1}) from three Muskoka–Haliburton area lakes (Red Chalk, Chub, Plastic) sampled on 13–19 occasions during the ice-free period of 1980 (N. D. Yan, unpubl. data).

The scarcity of preneutralization data and the paucity of information on the response of ciliates to acidification make evaluation of the Bowland Lake ciliate data very difficult. The common occurrence of several taxa, including *Vorticella* and *Mesodinium*, only after neutralization suggests improved conditions for some taxa. It appears that ciliates, like rotifers, increased after 1983 (Fig. 2) in parallel with the decline in crustaceans. The importance of a large peritrich ciliate (tentatively identified as *Campanella* sp.) before neutralization (Table 4) is unusual for lake plankton. It is interesting that *Campanella* disappeared after neutralization, but again was observed from 1986 on, perhaps reflecting early reacidification of the lake. Gilbert (1989) reported that *Campanella* and several rotifer species were depressed by *Daphnia*, while in Bowland Lake, *Campanella* was absent when abundances of large crustaceans, notably *H. gibberum*, were reduced. The ciliate fauna was not unusual otherwise.

The average annual densities of ciliates during the ice-free period (1.1×10^3 to 4.3×10^3 animals·L^{-1}, respectively) were lower than the range of 15×10^3 to 37×10^3 animals·L^{-1} reported by Gates (1984) for central Ontario lakes or the average density (10.8×10^3 animals·L^{-1}) reported by Beaver and Crisman (1982) for oligotrophic Florida lakes. However, our data combine depths and seasons, rather than just the summer epilimnion as sampled by Gates (1984), so direct comparison is inappropriate.

Changes in overall zooplankton abundance appeared to be related to predatory interactions with fish and *Chaoborus*, supporting previous suggestions that many differences between invertebrate communities in acidified and circumneutral lakes are related to the disappearance of fish and abundance of invertebrate predators, rather than a direct effect of altered chemistry (Eriksson et al. 1980; Yan et al. 1982; Henrikson et al. 1984; Yan and Geiling 1985). Additional factors that may also be implicated in determining the observed temporal patterns of zooplankton abundance include substantial yearly weather fluctuations and generally improved phytoplankton food sources after neutralization.

Changes in zooplankton communities directly attributable to neutralization were primarily taxonomic in nature and were judged to be positive responses because they reflected a shift to taxa more representative of nonacidic conditions. Based on our results, rotifer communities apparently respond very quickly (within 1 yr) to neutralization, particularly through rapid expansion of apparently acid sensitive taxa, most of which are not likely to be completely eliminated by acidification. Recolonization by acid-sensitive crustacean species may take at least several years to commence, and complete recovery to typical assemblages may take much longer. During the reacidification of neutralized lakes, significant effects on rotifer and crustacean communities can be expected in the range of pH 5.5–6.0.

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References

ALMER, B., W. DICKSON, C. EKSTROM, E. HORNSTROM, AND U. MILLER. 1974. Effects of acidification on Swedish lakes. Ambio 3: 30–36.

ANDERSSON, G., H. BERGGREM, A. CRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

ARTS, M. T., AND W. G. SPRULES. 1989. Use of enclosures to detect the contribution of particular zooplankton to growth of young-of-the-year yellow perch (*Perca flavescens* Mitchell). Oecologia 81: 21–27.

BEAVER, J. R., AND T. L. CRISMAN. 1982. The trophic response of ciliated protozoans in freshwater lakes. Limnol. Oceanogr. 27: 246–253.

BRADT, P. T., M. B. BERG, D. S. BARRASSO, J. L. DUDLEY, D. E. ARNOLD, J. F. P. COTTER, P. B. MYERS JR., P. SITKOWSKI, AND R. N. WEISMAN. 1984. The biological impact of acid precipitation on Pocono Mountain lakes. Department of Biology, Lehigh University, Bethlehem, PA. 215 p.

BREHM, V. J., AND M. P. D. MEIJERING. 1982. On the sensitivity to low pH of some selected crustaceans (*Daphnia* and *Gammarus*, Crustacea). Arch. Hydrobiol. 95: 17–27. (In German)

BREZONIK, P. L., T. L. CRISMAN, AND R. L. SCHULZE. 1984. Planktonic communities in Florida softwater lakes of varying pH. Can. J. Fish. Aquat. Sci. 41: 46–56.

CARTER, J. C. H., W. D. TAYLOR, R. CHENGALATH, AND D. A. SCRUTON. 1986. Limnetic zooplankton assemblages in Atlantic Canada with special reference to acidification. Can. J. Fish. Aquat. Sci. 43: 444–456.

CARVALHO, G. E., AND H. G. WOLF. 1989. Resting eggs of lake — *Daphnia* 1. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. Freshwater Biol. 22: 459–470.

CHABOT, F., AND E. J. MALY. 1986. Variation in diet of yellow perch (*Perca flavescens*) in a Quebec reservoir. Hydrobiologia 137: 117–124.

COOPER, D. W. 1968. The significance level in multiple tests made simultaneously. Heredity 23: 614–617.

CRYER, M., G. PEIRSON, AND C. R. TOWNSEND. 1986. Reciprocal interactions between roach *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31: 1022–1038.

DESTASIO, B. T., JR. 1989. The seed bank of a freshwater crustacean: copepodology for the plant ecologist. Ecology 70: 1377–1389.

DILLON, P. J., K. H. NICHOLLS, B. A. LOCKE, E. DE GROISBOIS, AND N. D. YAN. 1988. Phosphorus–phytoplankton relationships in nutrient poor softwater lakes in Canada. Verh. Int. Ver. Limnol. 23: 258–264.

DODSON, S. I. 1981. Morphological variation of *Daphnia pulex* Leydig (Crustacea: Cladocera) and related species from North America. Hydrobiologia 83: 101–114.

ERIKSSON, M. O. G., L. HENRIKSON, B. I. NILSSON, G. NYMAN, H. G. OSCARSON, A. E. STENSON, AND K. LARSSON. 1980. Predator–prey relations important for the biotic changes in acidified lakes. Ambio 9: 248–249.

FRYER, G. 1985. Crustacean diversity in relation to the size of waterbodies: some facts and problems. Freshwater Biol. 15: 347–361.

GATES, M. A. 1984. Quantitative importance of ciliates in the planktonic biomass of lake ecosystems. Hydrobiologia 108: 233–238.

GILBERT, J. J. 1988. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects of zooplankton community structure. Limnol. Oceanogr. 33: 1286–1303.

1989. The effect of *Daphnia* interference on a natural rotifer and ciliate community: short-term bottle experiments. Limnol. Oceanogr. 34: 607–617.

GIRARD, R., AND R. A. REID. 1990. Dorset Research Centre lakes: sampling methodology (1986–89) and lake morphometry. Ontario Ministry of the Environment Data Report DR 90/4, Dorset, Ontario.

GUNN, J. M., J. G. HAMILTON, G. M. BOOTH, C. D. WREN, G. L. BEGGS, H. J. RIETVELD, AND J. R. MUNRO. 1990. Survival, growth and reproduction of lake trout (*Salvelinus namaycush*) and yellow perch (*Perca flavescens*) after neutralization of an acidic lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 47: 446–453.

HAVENS, K. 1990. *Chaoborus* predation and zooplankton community structure in a rotifer dominated lake. Hydrobiologia 198: 215–226.

HAVENS, K., AND J. DECOSTA. 1988. An experimental analysis of the acid sensitivity of the common planktonic rotifer *Keratella cochlearis*. Int. Rev. Gesamten Hydrobiol. 73: 407–416.

HENRIKSON, L., H. G. NYMAN, H. G. OSCARSON, AND J. A. E. STENSON. 1985. Changes in the zooplankton community after lime treatment of an acidified lake. Verh. Int. Ver. Limnol. 22: 3008–3013.

HENRIKSON, L., H. G. OSCARSON, AND J. A. E. STENSON. 1984. Development of the crustacean zooplankton community after lime treatment of the fishless Lake Gardsjon, Sweden. Inst. Freshwater Res. Drottningholm Rep. 61: 104–114.

HITCHIN, G. G., AND N. D. YAN. 1983. Crustacean zooplankton communities of Muskoka–Haliburton study lakes: methods and 1976–1977 data. Ontario Ministry of the Environment Data Report DR 83/4, Toronto, Ont.

HULTBERG, H., AND I. B. ANDERSSON. 1982. Liming of acidified lakes: induced long-term changes. Water Air Soil Pollut. 18: 311–331.

HURLBERT, S. H., AND M. S. MULLA. 1981. Impacts of mosquitofish (*Gambusia affinis*) predation of plankton communities. Hydrobiologia 83: 125–151.

JACKSON, M. B., E. M. VANDERMEER, N. LESTER, J. BOOTH, L. A. MOLOT, AND I. GRAY. 1990. Effects of neutralization and early reacidification on filamentous algae and macrophytes in Bowland Lake. Can. J. Fish. Aquat. Sci. 47: 432–439.

KEAST, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes 2: 53–70.

KELLER, W., D. P. DODGE, AND G. M. BOOTH. 1990a. Experimental lake neutralization program: overview of neutralization studies in Ontario. Can. J. Fish. Aquat. Sci. 47: 410–411.

KELLER, W., L. A. MOLOT, R. W. GRIFFITHS, AND N. D. YAN. 1990b. Changes in the zoobenthos community of acidified Bowland Lake after whole-lake neutralization and lake trout (*Salvelinus namaycush*) reintroduction. Can. J. Fish. Aquat. Sci. 47: 440–445.

KELLER, W., AND J. R. PITBLADO. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acid deposition. Water Air Soil Pollut. 23: 271–291.

KELLER, W., AND N. D. YAN. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

KELLER, W., N. D. YAN, K. HOLTZE, AND J. R. PITBLADO. 1990c. Inferred effects of lake acidification on *Daphnia galeata mendotae*. Environ. Sci. Technol. 24: 1259–1261.

KRUSKAL, J. B. 1964. Multidimensional scaling by optimising goodness of fit to a nonmetric hypothesis. Psychometrika 29: 1–27.

LYNCH, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253–272.

MACISAAC, H. J., T. C. HUTCHINSON, AND W. KELLER. 1987. Analysis of planktonic rotifer assemblages from Sudbury, Ontario, area lakes of varying chemical composition. Can. J. Fish. Aquat. Sci. 44: 1692–1701.

MACISAAC, H. J., W. KELLER, T. C. HUTCHINSON, AND N. D. YAN. 1986. Natural changes in the planktonic Rotifera of a small acid lake near Sudbury, Ontario following water quality improvements. Water Air Soil Pollut. 31: 791–797.

MALLEY, D. F., D. L. FINDLAY, AND P. S. S. CHANG. 1982. Ecological effects of acid precipitation on zooplankton, p. 297–327. *In* F. M. D'Itri [ed.] Acid precipitation: effects on ecological systems. Ann Arbor Science Publishers, Ann Arbor, MI.

MOLOT, L. A., P. J. DILLON, AND G. M. BOOTH. 1990a. Whole-lake and nearshore water chemistry in Bowland Lake, before and after treatment with $CaCO_3$. Can. J. Fish. Aquat. Sci. 47: 412–421.

MOLOT, L. A., J. G. HAMILTON, AND G. M. BOOTH. 1986. Neutralization of acidic lakes: short-term dissolution of dry and slurried calcite. Water Res. 20: 757–761.

MOLOT, L. A., L. HEINTSCH, AND K. H. NICHOLLS. 1990b. Response of phytoplankton in acidic lakes in Ontario to whole-lake neutralization. Can. J. Fish. Aquat. Sci. 47: 422–431.

MOORE, M. V., AND J. J. GILBERT. 1987. Age-specific *Chaoborus* predation on rotifer prey. Freshwater Biol. 17: 223–236.

NEILL, W. E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. Oecologia 61: 175–181.

NILSSEN, J. P., T. OSTDAHL, AND W. T. W. POTTS. 1984. Species replacements in acidified lakes: physiology, predation or competition. Inst. Freshwater Res. Drottningholm Rep. 61: 149–153.

NYBERG, P. 1984. Impact of *Chaoborus* predation on planktonic crustacean communities in some acidified and limed forest lakes in Sweden. Inst. Freshwater Res. Drottningholm Rep. 61: 154–166.

PATALAS, K. 1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, Northwestern Ontario. J. Fish. Res. Board Can. 28: 231–244.

PORCELLA, D. B. 1989. Lake acidification mitigation project (LAMP): an overview of an ecosystem perturbation experiment. Can. J. Fish. Aquat. Sci. 46: 246–248.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

SCHAFFNER, W. R. 1989. Effects of neutralization and addition of brook trout (*Salvelinus fontinalis*) on the limnetic zooplankton communities of two acidic lakes. Can. J. Fish. Aquat. Sci. 46: 295–305.

SCHINDLER, D. W. 1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Board Can. 26: 1948–1955.

SCHINDLER, D. W., K. H. MILLS, D. F. MALLEY, D. L. FINDLAY, J. A. SHEARER, I. J. DAVIES, M. A. TURNER, G. A. LINSEY, AND D. R. CRUIKSHANK. 1985. Long-term ecosystem stress: the effects of years of experimental acidification of a small lake. Science (Wash., DC) 228: 1395–1401.

SIEGFRIED, C. A., J. W. SUTHERLAND, S. O. QUINN, AND J. A. BLOOMFIELD. 1984. Lake acidification and the biology of Adirondack lakes. Verh. Int. Ver. Limnol. 22: 549–558.

SPRULES, W. G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

TAYLOR, W. D., AND M. L. HEYNEN. 1987. Seasonal and vertical distribution of Ciliophora in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2185–2191.

THRELKELD, S. T., AND E. M. CHOINSKI. 1987. Rotifers, cladocerans and planktivorous fish: what are the major interactions? Hydrobiologia 147: 239–243.

VON ENDE, C. N., AND D. DEMPSEY. 1981. Apparent exclusion of the cladoceran *Bosmina longirostris* by the invertebrate predator *Chaoborus americanus*. Am. Midl. Nat. 105: 240–248.

YAN, N. D. 1983. Effects of changes in pH on transparency and thermal regimes of Lohi Lake, near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 40: 621–626.

1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 43: 788–796.

YAN, N. D., AND P. J. DILLON. 1984. Experimental neutralization of lakes near Sudbury, Ontario, p. 417–456. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons, Inc., New York, NY.

YAN, N. D., AND W. GEILING. 1985. Elevated planktonic rotifer biomass in acidified metal-contaminated lakes near Sudbury, Ontario. Hydrobiologia 120: 199–205.

YAN, N. D., C. J. LAFRANCE, AND G. G. HITCHIN. 1982. Planktonic fluctuations in a fertilized, acidic lake: the role of invertebrate predators, p. 137–154. *In* R. E. Johnson [ed.] Acid rain/fisheries. Proc. Int. Symp. Acidic Precip. Fish. Impacts Northwest. North America. American Fisheries Society, Bethesda, MD.

YAN, N. D., W. A. SCHEIDER, AND P. J. DILLON. 1977. Chemical and biological changes in Nelson Lake, Ontario following experimental elevation of lake pH. Proc. Can. Symp. Water Pollut. Res. Can. 12: 213–231.

YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

Benthic Macroinvertebrate Changes in Lakes near Sudbury, Ontario, following a Reduction in Acid Emissions

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Benthic macroinvertebrates were sampled from three lake basins before and after a reduction in acidity, a result of reduced acid emissions from the smelting industry in Sudbury, Ontario. The number of taxa and macroinvertebrate density were greater in the later surveys of the lakes than expected by chance alone. Species richness and macroinvertebrate density were higher in all littoral habitats and in profundal habitats of two lake basins. Species richness showed little change and macroinvertebrate density was lower in the profundal habitat of the third lake basin. Increased survival, probably as a result of reduced chemical toxicity, best accounted for the higher species richness and benthic density. Trout predation, through a numerical response, probably masked these responses in the profundal habitat of the third lake basin because the refuge area from predation (i.e. region of the hypolimnion low in dissolved oxygen) was small. These data indicate that biological recovery of industrially acidified lakes is possible solely by reducing emissions, provided that recolonizing species are not locally extinct.

Des macroinvertébrés benthiques ont été prélevés des bassins de trois lacs avant et après une baisse de l'acidité des eaux découlant d'une réduction des émissions acides des fonderies de Sudbury (Ontario). Le nombre de taxons et la densité des macroinvertébrés notés au cours des relevés des lacs faits après la réduction des émissions étaient plus élevés que ne pouvait le laisser prévoir une variation due exclusivement au hasard. La diversité en espèces et la densité des macroinvertébrés étaient plus élevées dans tous les habitats littoraux et les habitats de la zone profonde des bassins de deux lacs. La richesse en espèces variait peu et la densité des macroinvertébrés était plus faible dans l'habitat profond du bassin du troisième lac. Une augmentation de la survie, probablement due à une réduction de la toxicité chimique, expliquait le mieux les valeurs plus élevées de la diversité des espèces et de la densité benthique. La prédation par les truites, de par une action numérique, a probablement masqué ces réponses dans l'habitat de la zone profonde du troisième lac car la zone assurant un refuge contre les prédateurs (région de l'hypolimnion pauvre en oxygène dissous) était peu importante. Ces données montrent que le rétablissement biologique des lacs acidifiés par les activités industrielles n'est possible que par la réduction des émissions et à la condition que les espèces permettant la recolonisation n'y soient pas disparues.

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Substantial reductions in sulphur and metal emissions from the smelting industry since the mid-1970s have resulted in general water chemistry improvements (e.g. reduced acidity, SO_4, and metal concentrations, increased alkalinity) in lakes surrounding Sudbury, Ontario (LaZerte and Dillon 1984; Keller and Pitblado 1986; Gunn and Keller 1990). The response of lentic biota to reduced emissions, however, is less clear. The species richness of limnetic crustacean and benthic macroinvertebrate communities increased in some lakes as a result of acid sensitive species establishing populations (Gunn and Keller 1990; Keller and Yan 1991). Furthermore, brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*) reestablished reproducing populations, either from stocked or remnant populations, in a few lakes where surface water pH has returned above 5.7 (Keller and Pitblado 1985; Gunn and Keller 1990; Keller and Yan 1991). Clearly, more information is needed regarding the natural response of lentic communities to reduced acidic deposition before an assessment can be made of the potential recovery of lake ecosystems as a consequence of reduced emissions.

We examined the response of littoral and profundal benthic macroinvertebrates to reduced acid emissions by comparing the density of individual macroinvertebrates in three lake basins (Whitepine Lake and northern and southern basins of Laundrie Lake; Fig. 1) before and after improvements in water chemistry conditions. Temporal comparisons within lakes, in contrast with spatial comparisons between lakes (e.g. Dermott 1985; Dermott et al. 1986), permit an examination of the response of lentic biota while standardizing for the effects of morphometry, sediment composition, and other confounding factors. Subsequently, we compared the response of benthic fauna to reduced acidity resulting from reduced acid emissions with that resulting from limestone addition (Keller et al. 1990).

Study Lakes

Whitepine Lake (47°17′N, 80°50′W) is a 67-ha, single-basin, headwater lake, with a volume of 3.8×10^6 m^3, maximum

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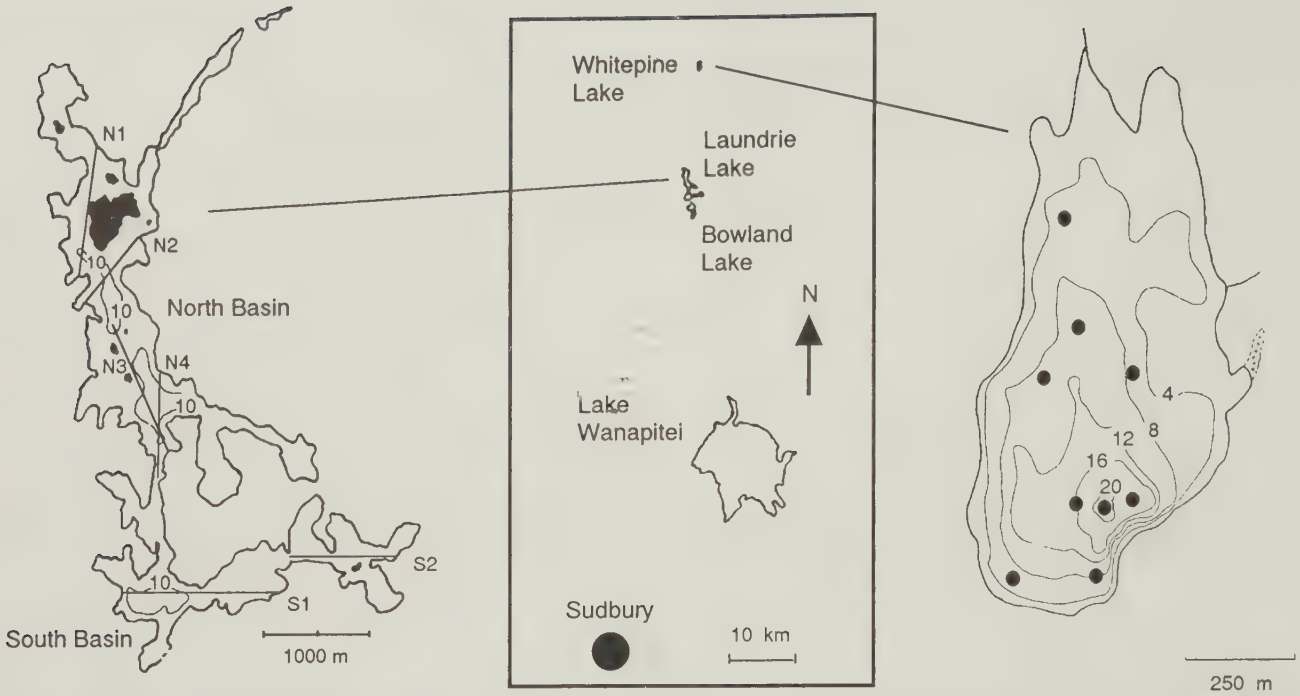

FIG. 1. Location of study lakes and sampling sites. For Laundrie Lake, sampling sites were located along four transects in the northern basin (N1–N4) and two transects in the southern basin (S1 and S2). For Whitepine Lake, sampling sites are indicated by black dots. Depth contours are in metres.

TABLE 1. Average lake water characteristics of the study lakes. Lakes were sampled on at least six occasions per year, except for the northern basin of Laundrie Lake in 1987. Values are expressed as $mg \cdot L^{-1}$, except for pH, colour, and Secchi depth. Where possible, data are provided for years adjacent to and during macroinvertebrate surveys. Data sources: Keller et al. (1992); Keller and Yan (1991); W. Keller (unpubl. data).

Lake	Year	pH	Alkalinity	Ca	Sulphate	Al	Secchi (m)	Colour (TCU)
Whitepine	1980	5.4	0.1	3.1	11.4	0.069	9.3	—
	1981	5.7	0.2	2.9	11.3	0.059	8.8	—
	1982	5.8	0.5	2.8	10.5	0.044	7.7	—
	1987	6.0	0.8	2.3	9.4	0.026	7.9	2.3
	1988	5.9	0.6	2.3	9.4	0.040	6.4	5.1
Laundrie, northern basin	1975	4.9	—	3.1	12.0	—	5.3	—
	1976	4.8	—	3.3	13.0	0.118	7.6	—
	1985	5.5	0.0	2.5	8.7	0.081	3.7	17.2
	1986	5.6	0.4	2.3	8.3	0.079	4.0	14.6
	1987[a]	5.5	0.6	2.3	7.3	0.074	5.9	14.0
Laundrie, southern basin	1975	5.1	—	3.7	12.9	—	7.6	—
	1976	5.1	—	3.7	13.5	0.115	8.3	—
	1985	6.0	0.6	2.7	9.2	0.044	5.0	8.7
	1986	6.0	0.9	2.6	8.5	0.043	5.8	7.5

[a]Only one sampling date.

depth of 22 m, and mean depth of 5.9 m, located about 90 km north of Sudbury, Ontario. It is dilute (conductivity $<40\ \mu S \cdot cm^{-1}$), clear (colour <10 TCU, Secchi depth >6 m), and oligotrophic (total phosphorus (TP) $<10\ \mu g \cdot L^{-1}$; dissolved organic carbon (DOC) $<3\ mg \cdot L^{-1}$), based on measurements for ice-free periods from 1980 to 1988 (W. Keller, unpubl. data). During late summer, the thermocline is between 8 and 12 m; the dissolved oxygen concentration drops below $5\ mg \cdot L^{-1}$ only in the small area where the depth exceeds 16 m (Gunn and Keller 1984).

From 1980 to 1988, water chemistry conditions markedly improved; pH increased from about 5.4 to 5.9, while sulphate and aluminum concentrations declined (Table 1). During these eight years, annual emissions of SO_2 declined from about 935×10^3 to 718×10^3 tonnes (Gunn and Keller 1990).

The fish community in the early 1980s was typical of an acid-stressed lake; yellow perch (*Perca flavescens*) was predominant, accompanied only by a few large, nonreproducing lake trout, burbot (*Lota lota*), and white sucker (*Catostomus commersoni*) (Gunn and Keller 1984). A few young lake trout, however, were collected in 1982 (Gunn and Keller 1990), indicating that chemical conditions had become sufficient for successful spawning. By 1987, the fish community was composed of a self-sustaining lake trout population and a small perch popu-

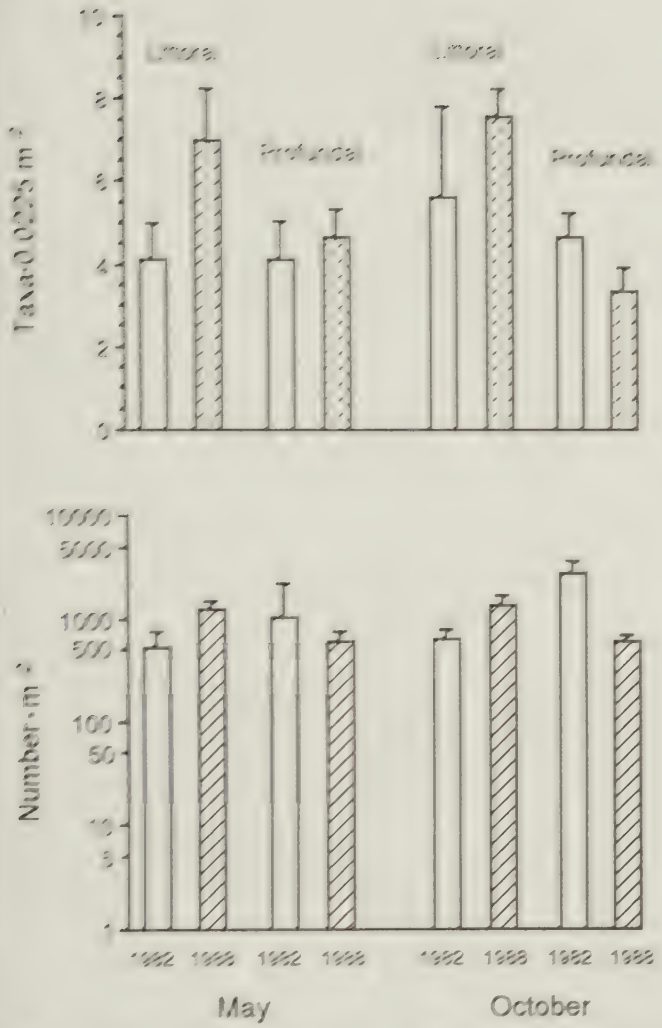

FIG. 2. Mean species richness (upper panel) and macroinvertebrate density (lower panel) in the littoral and profundal habitats of Whitepine Lake in May and October 1982 and 1988. Error bars represent 1 standard deviation.

lation (Gunn and Keller 1990), a fish community typical of a non-acid-stressed lake.

Laundrie Lake (47°07′N, 80°52′W), located about 72 km north of Sudbury, has a surface area of 364 ha and a volume of 18.3 × 10^6 m^3; maximum depth is 24 m and mean depth 4.9 m. The lake is dilute (conductivity <40 $\mu S \cdot cm^{-1}$), clear (colour <18 TCU), and oligotrophic (TP <10 $\mu g \cdot L^{-1}$; DOC <5 $mg \cdot L^{-1}$), based on periodic measurements for the ice-free periods from 1975 to 1986 (W. Keller, unpubl. data). The southern basin is consistently more alkaline and clearer than the northern basin (Table 1). During late summer, the thermocline is between 6 and 10 m; the dissolved oxygen concentration drops below 5 $mg \cdot L^{-1}$ where the depth exceeds 7 m in the northern basin and 14 m in the southern basin (J. M. Gunn, Ontario Ministry of Natural Resources, Sudbury, Ont., unpubl. data).

From 1975 to 1987, water chemistry conditions in both basins greatly improved; pH increased, while the sulphate and aluminum concentrations declined (Table 1). During these 12 years, annual emissions of SO_2 declined from about 1900 × 10^3 to 730 × 10^3 tonnes (Gunn and Keller 1990). While a substantial increase in pH had already occurred by 1983, the experimental neutralization of Bowland Lake, located directly upstream, in 1983 probably contributed to the reduction in acidity.

The fish community in the late 1970s was typical of an acid-stressed lake; yellow perch was predominant, accompanied by a few, large, native lake trout, white sucker, longnose sucker (*Catostomus catostomus*), and some small stocked lake trout (Kelso and Gunn 1984). Although the pH increased to 5.5 in the northern basin and near 6.0 in the southern basin by 1987, the fish community still reflected acid-stressed conditions; yellow perch was still predominant, accompanied by stocked lake trout and a few white sucker (J. M. Gunn, Ontario Ministry of Natural Resources, Sudbury, Ont., unpubl. data).

Methods

Benthic macroinvertebrates from Whitepine Lake were collected at six littoral and three profundal sampling sites (Fig. 1) in May and October 1982 and 1988. Three samples were collected at each site with a 15 × 15 cm Ekman grab and sieved through a 600-μm-mesh screen; the retained sediment, debris, and organisms were preserved with 10% buffered formalin. Invertebrates were later sorted, identified to the lowest possible taxon, and stored in 80% ethanol.

Benthic invertebrates from Laundrie Lake were collected at 25 sites along four transects in the northern basin and 17 sites along two transects in the southern basin in 1975 (Fig. 1), using a 15 × 15 cm Ekman grab. Sites along three transects were sampled on June 10 and along the other transects on July 29. In 1987, 21 sites along the same four transects in the northern basin and 13 sites along the same two transects in the southern basin were sampled October 14–17 using the same technique. Sampling sites in 1987 were located at the same water depths as the 1975 sites. Single samples were collected at each site in 1975 whereas two samples were collected per site in 1987. Samples were processed in the same manner as described for Whitepine Lake.

The invertebrates were identified by the first author for both surveys of Laundrie Lake, the 1982 survey of Whitepine Lake, and diet analysis of fish from Whitepine and Laundrie lakes. The taxonomy of the final survey of Whitepine Lake was corrected from the available specimens by the first author to standardize the data. In Laundrie Lake, three species groups of *Chironomus* were identified: *Chironomus salinarius*-gp denoted those with no ventral abdominal gills, *Chironomus attenuatus*-gp denoted those with abdominal gills and lateral projections on the seventh abdominal segment, and *Chironomus* sp. denoted those with abdominal gills only. Species groups of *Chironomus* were not identified in Whitepine Lake. Similarly, specimens of *Psectrocladius* (s.l.) were further identified as *Monopsectrocladius*, *Mesopsectrocladius*, or *Psectrocladius* (s.s.) in Laundrie whereas specimens of *Psectrocladius* (s.l.) from Whitepine Lake were not available for further identification. These few differences in taxonomy between lakes had no effect on the outcome of the analysis.

To evaluate the biological response of benthos to the reduced acidity and improved water chemistry, the benthic fauna in the littoral and profundal habitats of each lake was compared between surveys. The depth separating littoral and profundal habitats in each lake was estimated from Secchi depth, depth of the thermocline, and macroinvertebrate distributions. The profundal habitat was characterized by the predominance of *Chaoborus*, *Chironomus*, and *Sergentia* whereas the littoral zone was characterized by a diversity of insects: alderflies, caddisflies, mayflies, dragonflies, orthoclads, and beetles.

TABLE 2. Summary of repeated-measures ANOVA for Whitepine Lake to test (A) H_0: mean number of littoral taxa in 1982 equals that of 1988 and (B) H_0: mean density of littoral macroinvertebrates in 1982 equals that of 1988. Sampling sites were treated as subjects; seasons (May and October) and the triplicate samples were treated as trials. $*p < 0.05$; $**p < 0.01$; NS, $p > 0.05$.

		Hypothesis A		Hypothesis B	
Source of variation	df	MS	*F*	MS	*F*
Between subjects effects					
Year	1	105.13	11.04*	12.42	37.15**
Site	5	3.75	0.39 NS	0.15	0.15 NS
Year·site	5	9.53		0.33	
Within subjects effects					
Trial factor 1					
Seasons	1	19.01	5.36 NS	0.01	0.03 NS
Seasons·year	1	4.01	1.13 NS	0.01	0.02 NS
Seasons·site	5	6.21	1.75 NS	0.45	0.96 NS
Seasons·year·site	5	3.55		0.47	
Trial factor 2					
Samples	2	0.93	0.18 NS	0.08	0.20 NS
Samples·year	2	1.63	0.32 NS	0.24	0.64 NS
Samples·site	10	1.93	0.38 NS	0.29	0.78 NS
Samples·year·site	10	5.13		0.38	
Trials interaction					
Seasons·samples	2	2.26	0.48 NS	0.17	0.43 NS
Seasons·samples·year	2	4.18	0.89 NS	0.38	0.97 NS
Seasons·samples·site	10	1.36	0.19 NS	0.26	0.68 NS
Seasons·samples·year·site	10	4.71		0.39	

A repeated-measures ANOVA was used to test two hypotheses: (A) mean number of taxa in Whitepine Lake was not different between survey years and (B) the mean density of macroinvertebrates in Whitepine Lake was not different between survey years. Sampling months and the triplicate samples collected at a site were treated as trials, while sampling sites were treated as subjects. A separate test was conducted for littoral and profundal habitats.

A two-way, mixed model ANOVA was used to test the two hypotheses stated above for Laundrie Lake. Sampling sites were treated as blocks; the mean of duplicate samples collected at each site in 1987 was compared against the single sample collected at each site in 1975. A separate test was conducted for littoral and profundal habitats.

To determine if a species was absent during either the initial or final survey or was simply not detected because of the sampling design, a 95% detection limit (i.e. the minimum density that provides a 95% chance of detection) was estimated for each habitat in Whitepine and Laundrie lakes based on the sampling design. For example, 14 Ekman grab samples, totalling an area of 0.32 m^2, were collected from the littoral habitat of the southern basin of Laundrie Lake in 1975. Thus, a 95% detection limit (D) can be estimated from the inequality

$$(1 - 0.32)^D < 0.05.$$

In this case, D is about 8 animals·m^{-2}. Thus, for species with an average density of 8·m^{-2} or greater, there is a 95% chance of collecting at least one animal with 14 Ekman grabs. Taxa, therefore, whose estimated abundance was 8·m^{-2} or greater in the initial survey were considered to have disappeared from the lake if they were not collected in the final survey. Taxa whose estimated abundance was less than 8·m^{-2} in the initial survey, however, were considered to have simply been missed if they were not collected in the final survey.

All analyses were conducted using SYSTAT (Wilkinson 1987). Densities were log-transformed before statistical comparisons were conducted.

Results

Whitepine Lake

There was no consistent difference in the relative abundance of insects (61–81%), molluscs (8–21%), or annelids (6–20%) in the littoral habitat between seasons (May versus October) or years (1982 versus 1988). *Dicrotendipes, Procladius, Pisidium,* and *Rhyacodrilus montana* (Brinkhurst) always accounted for >50% of the macroinvertebrates.

Species richness (number of taxa per sample) in the littoral habitat (Fig. 2) was higher in 1988 than in 1982 ($p < 0.02$) in both seasons (p(season–year interaction) > 0.34) (Table 2). Thirty-three taxa were present in 1988, while only 26 taxa were found in 1982 (Table 3). Twelve taxa, which included the mayfly *Hexagenia,* the caddisfly *Polycentropus*, five midges, and five oligochaetes, only occurred in 1988; only seven taxa, however, were considered to have colonized the lake between surveys (Table 4). Meanwhile, five macroinvertebrate taxa were not recollected in the final survey (two caddisflies and three midges); only two taxa, however, were considered to have disappeared between surveys (Table 4).

Density of littoral macroinvertebrates (Fig. 2) was higher in 1988 than in 1982 ($p < 0.002$) in both seasons (p(season–year interaction) > 0.88) (Table 2). The density of those taxa present in the initial survey approximately doubled in the final survey in each season. The density of three taxa, *Dicrotendipes, Phaenopsectra,* and *Tanytarsus*, was markedly higher (i.e. more than three times) in 1988 (Table 3). Seventeen taxa showed relatively little change in density between sampling years, while only the density of *Glyptotendipes* was markedly lower in 1988.

TABLE 3. Change (response) in macroinvertebrate occurrence and density between survey years in the littoral habitat of Whitepine and Laundrie lakes. Depth of the littoral habitat is noted in parentheses below each lake. +, taxon collected only on final survey; −, taxon collected only on initial survey; >, density of taxon on final survey was more than three times that of initial survey; <, density of taxon on final survey was less than a third of that of initial survey; ø, no change between surveys; no entry, taxon was not present in either survey.

Response	Invertebrate taxa	Whitepine (<12 m)	Laundrie northern basin (<8.25 m)	Laundrie southern basin (<8.25 m)
Positive	*Tanytarsus*	>	>	>
	Dicrotendipes	>	>	>
	Nilothauma	+	+	>
	Arcteonais lomondi	+	+	+
	Slavina appendiculata	+	+	+
	Phaenopsectra	>		+
	Sergentia		+	+
	Triaenodes		+	+
	Chironomus attenuatus-gp		+	+
	Cladotanytarsus		+	+
	Hydrobaenus		+	+
	Musculium securis		+	+
	Aulodrilus pigueti	+		+
	Specaria josinae		+	+
	Procladius	ø	>	>
	Pisidium	ø	+	>
	Polypedilum	+	ø	>
	Stylaria lacustris	ø	+	+
	Aulodrilus americanus	ø	+	+
	Psectrocladius	ø	+	+
	Agrypnia	ø	+	+
	Pagastiella			+
	Nectopsyche			+
	Hydratophylax argus			+
	Somatochlora			+
	Tetragoneuria			+
	Ladona julia			+
	Gomphus			+
	Hexagenia	+		
	Paraleptophlebia		+	
	Chaoborus flavicans			+
	Tribelos			+
	Mesopsectrocladius			+
	Clinotanypus			+
	Conchapelopia			+
	Hyalella azteca			+
	Dero nivea	+		
	Uncinais uncinata		+	
	Chironomus salinarius-gp			+
	Vejdovskyella comata			+
	Oecetis		ø	+
	Chaoborus punctipennis	ø	>	ø
	Ablabesmyia	ø	ø	>
	Microtendipes	ø	+	ø
Null	*Sialis*	ø	ø	ø
	Phylocentropus	ø	ø	ø
	Ceratopogonidae	ø	ø	ø
	Crytochironomus	ø	ø	ø
	Monopsectrocladius		ø	ø
	Micropsectra	ø		
	Paracladopelma	ø		
	Rhycodrilus montana	ø		
Variable	*Polycentropus*	+	+	<
	Chironomus sp.	+	<	<
	Lumbriculus variegatus	+	<	−
	Paratanytarsus	+		−
	Pseudochironomus	+	−	−

TABLE 3. (*Concluded*)

Response	Invertebrate taxa	Whitepine (<12 m)	Laundrie northern basin (<8.25 m)	Laundrie southern basin (<8.25 m)
Variable	*Molanna*	−	+	+
	Zalutschia	−	+	>
	Heterotanytarsus	−	+	
Negative	*Glyptotendipes*	<		
	Deronectes		−	
	Dineutus			−
	Phryganea	−		
	Cryptotendipes		−	
	Hanischia			−
	Chrysops		−	
	Ophidonais serpentina		−	
	Limnodrilus claparedianus		−	
	Protanypus	ø	<	−
	Cladopelma		−	−
	Limnodrilus hoffmeisteri		−	−
	Heterotrissocladius	−	−	−

TABLE 4. Change in occurrence between surveys years in the littoral habitat of Whitepine and Laundrie lakes of taxa that have a 95% chance of being detected in the year they were absent (see Methods). + indicates that the taxon invaded the lake between survey years; − indicates that the taxon disappeared from the lake between survey years. For Laundrie Lake, the change in occurrence of taxa is noted for both basins; parentheses indicate that the taxon had a <95% chance of being detected.

	Whitepine	Laundrie northern basin	Laundrie southern basin
Arcteonais lomondi	+	+	+
Chironomus sp.	+		
Dero nivea	+		
Aulodrilus pigueti	+		
Polypedilum	+		
Pisidium		+	
Triaenodes		+	(+)
Cladotanytarsus		+	(+)
Sergentia		+	(+)
Aulodrilus americanus		+	(+)
Stylaria lacustris		+	+
Chironomus attenuatus-gp		(+)	+
Hydrobaenus		(+)	+
Psectrocladius (s.s.)		(+)	+
Musculium securis		(+)	+
Dragonflies			+
Hyalella azteca			+
Pseudochironomus	+	−	−
Lumbriculus variegatus	+		−
Heterotrissocladius	−	−	−
Limnodrilus hoffmeisteri		−	−
Chrysops		−	
Cryptotendipes		−	
Ophidonais serpentina		−	
Limnodrilus claparedianus		−	
Cladopelma		(−)	−
Protanypus			−
Paratanytarsus			−
Heterotanytarsus	−		

The relative abundance of insects in the profundal habitat was lower in 1988 (55–80%) than in 1982 (91–92%). Conversely, the proportion of annelids was higher in 1988 (20–33%) than in 1982 (8–9%), and the proportion of molluscs was also higher in 1988 (0–12%) than in 1982 (0%). *Sergentia, Chironomus* sp., and *Chaoborus punctipennis* (Say) accounted for >50% of benthos in each season of 1982 whereas *C. punctipennis* and *Rhycodrilus montana* similarly predominated in each season of 1988.

Species richness in the profundal habitat (Fig. 2) was not different between years ($p > 0.57$) in either season (p(season–year interaction) > 0.12) (Table 5). Twelve taxa were present in 1988 and eight taxa in 1982 (Table 6). Six taxa, four true flies, the bivalve *Pisidium*, and the worm *Limnodrilus hoffmeisteri* Claparede, only occurred in 1988; only *Pisidium*, however, was considered to have invaded the lake between sampling years. Two taxa, a riffle beetle and *Dicrotendipes*, were not recollected in 1988; only *Dictrotendipes*, however, was considered to have disappeared between sampling years.

The density of profundal macroinvertebrates (Fig. 2) was lower ($p < 0.04$) in 1988 than in 1982 in each season (p (season–year interaction) > 0.14) (Table 5). The density of those taxa present in the initial survey was 60 and 80% lower in May and October of the final survey, respectively. The markedly lower density of *Sergentia* and *Chironomus* sp. primarily accounted for the lower macroinvertebrate density in 1988. No taxa present in 1982 had a higher density in 1988, while the density of four taxa was similar between sampling years (Table 6).

Northern Basin of Laundrie Lake

The relative abundance of insects (73–75%) and annelids (21–25%) in the littoral habitat varied little between years; molluscs were absent in 1975 but composed 6% of the macroinvertebrates in 1987. *Heterotrissocladius, Procladius, Chironomus* sp., *C. punctipennis, Lumbriculus variegatus* (Muller), and *L. hoffmeisteri* accounted for >50% of the benthos in 1975, while *Procladius, C. punctipennis, Tanytarsus*, and *Aulodrilus americanus* Brinkhurst and Cook similarly predominated in 1987.

TABLE 5. Summary of repeated-measures ANOVA for Whitepine Lake to test (A) H_0: mean number of profundal taxa in 1982 equals that of 1988 and (B) H_0: mean density of profundal macroinvertebrates in 1982 equals that of 1988. Sampling sites were treated as subjects; seasons (May and October) and the triplicate samples were treated as trials. $*p < 0.05$; $**p < 0.01$; NS, $p > 0.05$.

		Hypothesis A		Hypothesis B	
Source of variation	df	MS	*F*	MS	*F*
Between subjects effects					
Year	1	1.36	0.45 NS	9.11	20.56**
Site	2	0.194	0.06 NS	0.14	0.32 NS
Year·site	2	3.03		0.44	
Within subjects effects					
Trial factor 1					
Seasons	1	1.36	1.14 NS	1.99	4.54 NS
Seasons·year	1	8.03	6.72 NS	2.52	5.76 NS
Seasons·site	2	1.69	1.42 NS	1.10	2.53 NS
Seasons·year·site	2	1.19		0.44	
Trial factor 2					
Samples	2	0.19	0.61 NS	0.03	0.31 NS
Samples·year	2	2.53	7.91*	0.10	0.95 NS
Samples·site	4	1.65	5.17 NS	0.25	2.32 NS
Samples·year·site	4	0.32		0.11	
Trials interaction					
Seasons·samples	2	0.86	1.77 NS	0.09	0.34 NS
Seasons·samples·year	2	2.19	4.51 NS	0.14	0.54 NS
Seasons·samples·site	4	1.32	2.71 NS	0.08	0.30 NS
Seasons·samples·year·site	4	0.49		0.27	

Species richness in the littoral habitat (Fig. 3) was higher in 1987 than in 1975 ($F = 12.3$; df = 1,9; $p < 0.007$). Thirty-seven macroinvertebrate taxa were found in 1987, while only 24 taxa were present in 1975 (Table 3). Twenty-two taxa, which included the mayfly *Paraleptophlebia*, the bivalves *Musculium securis* (Prime) and *Pisidium*, four caddisflies, nine midges, and six worms, occurred only in 1987; only seven taxa, however, were considered to have colonized the lake between surveys (Table 4). Nine taxa, which included the beetle *Dero-nectes*, five true flies, and three worms, were not recollected in 1987; seven of these were considered to have disappeared between surveys (Table 4).

Density of littoral invertebrates (Fig. 3) was higher in 1987 than in 1975 ($F = 7.89$; df = 1,9; $p < 0.02$). The density of those taxa present in the initial survey was about 30% greater in the final survey. The density of *C. punctipennis, Dicroten-dipes, Tanytarsus*, and *Procladius* was markedly higher in 1987, while that of *Chironomus* sp., *Protanypus*, and *L. variegatus* was markedly lower (Table 3). Eight taxa showed relatively little change between surveys.

The relative abundance of insects in the profundal habitat was higher in 1987 (93%) than in 1975 (76%). Molluscs were absent in 1975 and accounted for <1% of the benthos in 1987; the proportion of annelids was thus lower in 1987 (6%) than in 1975 (24%). *Chaoborus punctipennis, Chironomus* sp., and *C. salinarius*-gp accounted for >50% of benthos in 1975 and along with *Sergentia* similarly predominated in 1987.

Species richness in the profundal habitat (Fig. 3) was higher in 1987 than in 1975 ($F = 22.7$; df = 1,10; $p < 0.001$). Twenty-two taxa occurred in 1987, while only 11 taxa were present in 1975 (Table 6). Fifteen additional taxa, which included the caddisflies *Agrypnia* and *Polycentropus*, the bivalve *Pisidium*, eight true flies, and four oligochaetes, were found in 1987; *Pisidium, Chaoborus flavicans, C. attenu-atus*-gp, *Sergentia*, and *Stylaria lacustris* Linnaeus were considered to have invaded the lake between surveys. Three true flies and the worm *L. variegatus* were not recollected in 1987; only *L. variegatus*, however, was considered to have disappeared between surveys.

Density of profundal invertebrates (Fig. 3) was higher in 1987 than in 1975 ($F = 50.4$; df = 1,10; $p < 0.001$). The density of those taxa present in the initial survey was about 520% greater in the final survey. The density of *C. punctipennis* and *Procladius*, in particular, was markedly higher in 1987 than in 1975 (Table 6). Five taxa showed relatively little change in density between surveys; no taxa present in 1975 had a lower density in 1987.

Southern Basin of Laundrie Lake

The relative abundance of insects in the littoral habitat was lower in 1987 (61%) than in 1975 (90%). In contrast, the relative abundance of molluscs was higher in 1987 (8%) than in 1975 (1%), and similarly, that of annelids was higher in 1987 (28%) than in 1975 (8%). Crustaceans were absent in 1975 but accounted for 3% of benthos in 1987. *Chaoborus punctipennis* and the midges *Chironomus* sp., *Ablabesmyia, Paratanytarsus*, and *Procladius* composed >50% of macroinvertebrates in 1975, while *Pisidium, S. lacustris, Tanytarsus, Ablabesmyia*, and *Procladius* similarly predominated in 1987.

Species richness in the littoral habitat (Fig. 3) was higher in 1987 than in 1975 ($F = 39.6$, df = 1,9; $p < 0.001$). Forty-nine taxa occurred in 1987, while only 26 taxa were present in 1975. Thirty-two taxa, which included the bivalve *M. securis*, the crustacean *Hyalella azteca* (Saussure), six caddisflies, four dragonflies, 13 true flies, and seven oligochaetes, only occurred in 1987; only eight taxa, however, were considered to have colonized the lake between surveys (Table 4). Meanwhile, nine taxa, which included the beetle *Dineutus*, six midges, and two worms, were not recollected in 1987; seven of these were considered to have disappeared between surveys (Table 4).

TABLE 6. Change (response) in macroinvertebrate occurrence and density between survey years in the profundal habitat of Whitepine and Laundrie lakes. Depth of the profundal habitat is noted in parentheses below each lake. +, taxon collected only on final survey; −, taxon collected only on initial survey; >, density of taxon on final survey was more than three times that of initial survey; <, density of taxon on final survey was less than a third of that of initial survey; ø, no change between surveys; no entry, taxon was not present in either survey.

Response	Invertebrate taxa	Whitepine (>14 m)	Laundrie northern basin (>8.25 m)	Laundrie southern basin (>8.25 m)
Positive	*Pisidium*	+	+	
	Chaoborus flavicans		+	+
	Chironomus attenuatus-gp		+	+
	Ablabesmyia		+	+
	Chaoborus punctipennis	ø	>	>
	Rhyacodrilus montana	ø	+	+
	Micropsectra	+		
	Paracladopelma	+		
	Tanytarsus		+	
	Agrypnia		+	
	Polycentropus		+	
	Hydrobaenus		+	
	Monopsectrocladius		+	
	Conchapelopia		+	
	Arcteonais lomondi		+	
	Stylaria lacustris		+	
	Hyalella azteca			+
	Limnodrilus hoffmeisteri	+	ø	
	Procladius	ø	>	ø
	Limnodrilus claparedianus	ø	+	
	Microtendipes		ø	+
	Zalutschia		ø	+
Null	*Chironomus salinarius*-gp		ø	ø
Variable	Ceratopogonidae	+	−	−
	Heterotrissocladius	+	−	
	Chironomus sp.	<	ø	+
	Sergentia	<	+	ø
Negative	Elmidae	−		
	Dicrotendipes	−		
	Psectrocladius		−	
	Lumbriculus variegatus		−	
	Protanypus			−

Density of littoral invertebrates (Fig. 3) was higher in 1987 than in 1975 ($F = 18.0$; df = 1,0; $p < 0.002$). The density of those taxa present in the initial survey was about 150% greater in the final survey. The density of *Pisidium* and seven midges was markedly higher in 1987 compared with 1975, while that of *Polycentropus* and *Chironomus* sp. was markedly lower (Table 3). Seven taxa showed relatively little change between surveys.

Insects composed all profundal fauna in 1975. In 1987, insects still predominated (98%), but crustaceans and annelids accounted for <1 and 2% of benthos, respectively. *Chaoborus punctipennis, Sergentia,* and *C. salinarius*-gp accounted for most of the macroinvertebrates in 1975 and along with *Chironomus* sp. and *C. attenuatus*-gp similarly predominated in 1987.

Species richness in the profundal habitat (Fig. 3) was higher in 1987 than in 1975; this difference, however, was not significant ($F = 2.8$; df = 1,2; $p > 0.24$), possibly because of the low power afforded by the sampling design. Twelve taxa occurred in 1987 whereas only six were present in 1975 (Table 6). Eight taxa occurred only in 1987; *C. flavicans, C. attenuatus*-gp, *Zalutschia,* and *R. montana* were considered to have invaded the lake between surveys. Two true flies were not recollected in 1987; only *Protanypus* was considered to have disappeared between surveys.

Density of profundal invertebrates (Fig. 3) was higher in 1987 than in 1975 ($F = 28.7$; df = 1,2; $p < 0.03$). The density of those taxa present in the initial survey was about 200% greater in the final survey. The density of *C. punctipennis*, in particular, was markedly higher in 1987 than in 1975. Three taxa showed relatively little change in density between surveys, and no taxa present in 1982 had a lower density in 1987 (Table 6).

Discussion

The distribution and abundance of benthic macroinvertebrates are affected by various physical, chemical, and biotic factors. Effects of acidity on lentic benthos thus have been difficult to elucidate from survey studies (e.g. Dermott 1985; Dermott et al. 1986) because of the confounding influence of other factors (e.g. substrate composition, lake morphometry, water

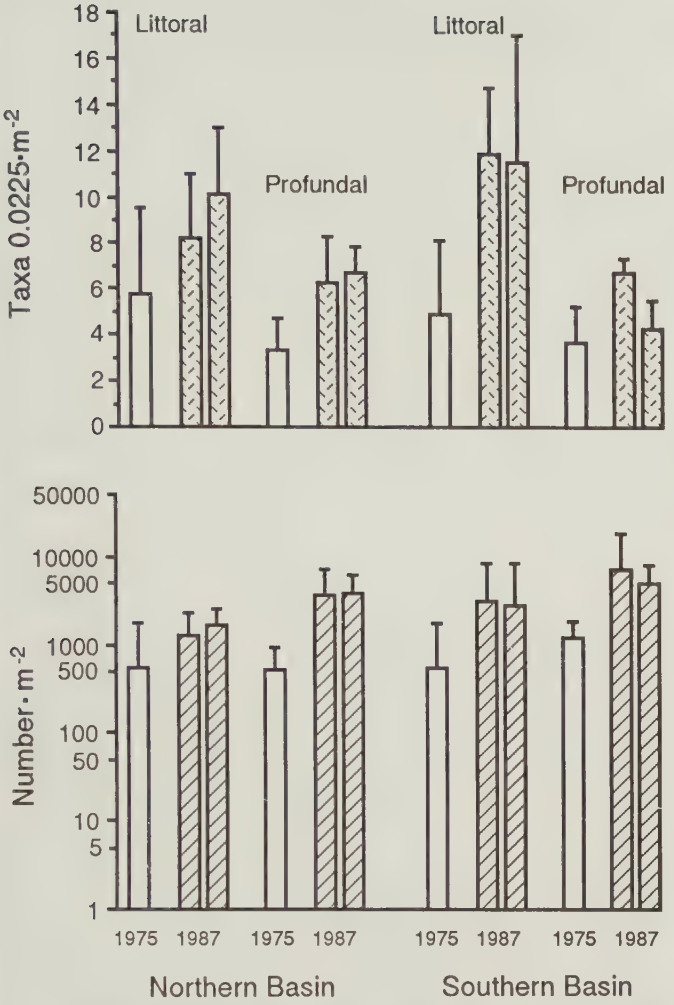

FIG. 3. Mean species richness (upper panel) and macroinvertebrate density (lower panel) in the littoral and profundal habitats of the northern and southern basins of Laundrie Lake in July 1975 and October 1987. For 1987, each bar represents the mean of one sample from each sampling site. Error bars represent 1 standard deviation.

chemistry, productivity, vertebrate predation). Effects of confounding factors, however, are minimized when comparing biota from the same lake before and after a change in acidity, resulting either from reduced acid emissions or experimental neutralization. Still, relating any nonrandom response to a change that occurred during a time interval must be done cautiously (Carpenter 1990).

Changes in occurrence (number of taxa) and density were observed for many macroinvertebrates in both the littoral and profundal habitats of Whitepine and Laundrie lakes between surveys (Tables 3 and 6). A seasonal effect may be partially responsible for some of these differences in Laundrie Lake, as the initial survey was conducted in early summer while the final was conducted in early autumn. However, there were no significant differences in species richness or invertebrate density in the littoral or profundal habitats of Whitepine Lake between May and October in either survey year (Tables 2 and 5). Furthermore, species richness and invertebrate density in August 1982 were not different from those in May or October of the same year (Fig. 4). Relative abundance (percent) of major invertebrate groups was also comparable in each habitat between seasons (Fig. 4). *Procladius, Pisidium*, and *R. montana* were numerically predominant in the littoral habitat of the

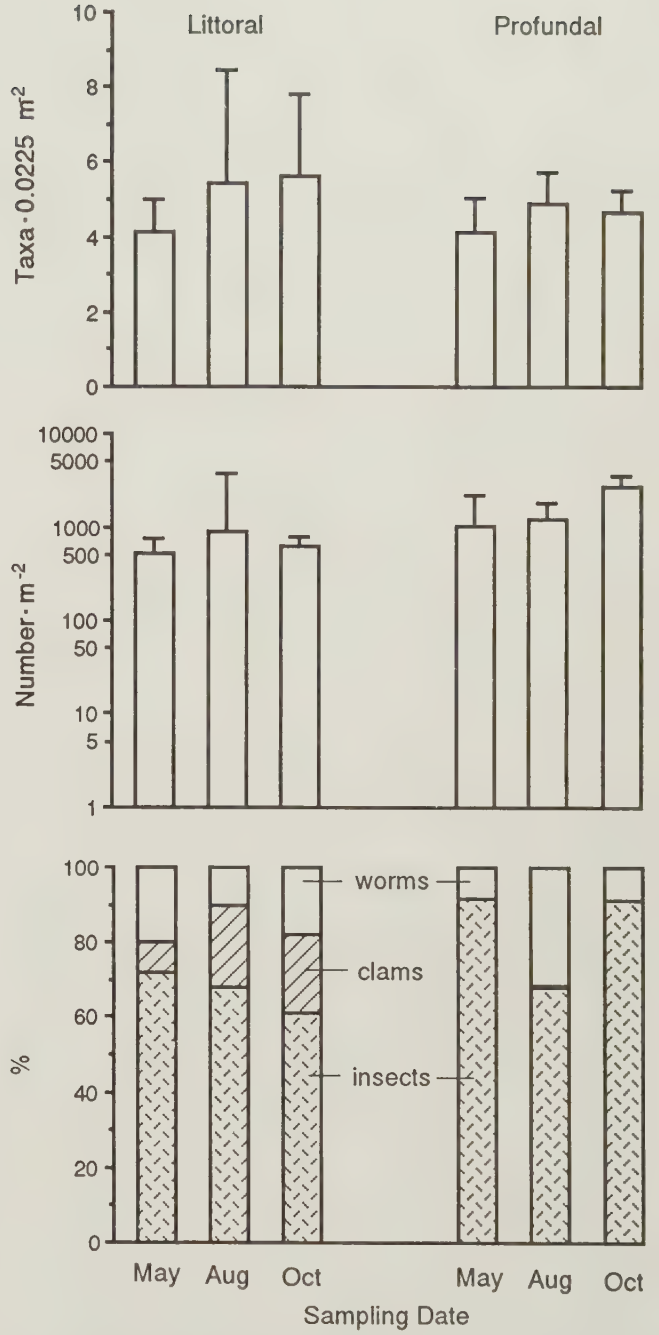

FIG. 4. Mean species richness (top panel), macroinvertebrate density (centre panel), and relative abundance of taxa (bottom panel) in the littoral and profundal habitats of Whitepine Lake in May, August, and October 1982. Error bars represent 1 standard deviation.

lake in all three sampling months. Similarly, *Chironomus, C. punctipennis*, and *Sergentia* numerically predominated in the profundal habitat in all sampling months. Seasonal variation in species richness and invertebrate density of acid-stressed lakes thus appear to be relatively minor given the sampling protocol. We concluded, therefore, that data collected from Laundrie Lake in the summer of 1975 were reasonable approximations for October and thus comparable with data collected in October 1987.

To determine if changes in macroinvertebrate occurrence and density could simply be explained by chance, their individual responses (Tables 3 and 6) were categorized into seven classes. Taxa whose density in the final survey was markedly greater

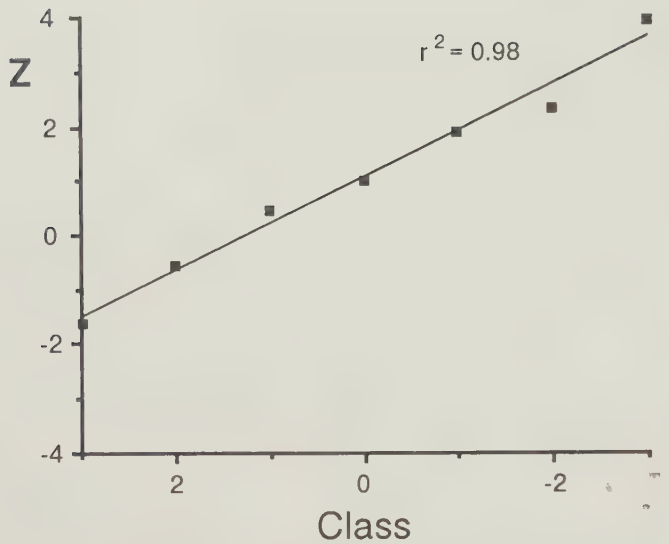

FIG. 5. Cumulative frequency, converted to standard normal deviates (Z), of individual macroinvertebrate responses ($n = 93$) in Whitepine and Laundrie lakes between surveys (see Tables 3 and 6). Class represents the number of lake basins taxa increased (3, 2, 1) or decreased (-1, -2, -3) in density (see Discussion). Class 0 represents taxa that showed little change in density between surveys.

than that in the initial survey in three, two, or one of the lake basins were placed into class 3, 2, or 1, respectively. Similarly, taxa whose density in the final survey was markedly less than that in the initial survey in three, two, or one of the lake basins were placed into class -3, -2, or -1, respectively. Taxa whose density was similar, i.e. did not differ more than a factor of 3, between surveys were placed in class 0, while taxa that showed opposite responses among the lake basins were not classified. A probability plot of cumulative frequency of classes fell along a straight line (Fig. 5), suggesting that the responses followed a normal distribution. The mean response, however, was greater than zero ($t = 6.34$; df $= 92$; $p < 0.001$), which indicates that both the number of taxa and number of macroinvertebrates with a higher density were greater in the final surveys than expected solely by chance.

The above analysis suggests that survival rates of established and colonizing species were greater in the final survey years. Higher survival rates possibly were a direct consequence of reduced acidity and improved water chemistry conditions. Aquatic invertebrates are known to vary in their sensitivity to acidity (Haines 1981), with more species living in near neutral waters than in acidic waters (Roff and Kwiathowski 1977; Wiederholm and Eriksson 1977; Mossberg and Nyberg 1979; Raddum and Saether 1981). A higher number of taxa were present in the littoral and profundal habitats of both lakes in the final surveys. Of the 19 (Table 4) and seven taxa that invaded the littoral and profundal habitats of the lakes, respectively, at least seven, *Arcteonais lomomdi, S. lacustris, Dero nivea, Cladotanytarsus, H. azteca, M. securis*, and *Pisidium*, are considered acid sensitive (Wiederholm and Eriksson 1977; Haines 1981; Eriksson et al. 1983; Walker et al. 1985; Dermott et al. 1986; Stephenson and Mackie 1986; Johnson and McNeil 1988), showing that acidic conditions in the lakes had been alleviated sufficiently between surveys for these species to finally survive and reproduce. The greater density of acid-tolerant species (i.e. taxa present in the initial survey) in the final surveys further suggests that survival rates of macroinvertebrates were higher in the final surveys as a result of improved chemical conditions (Hultberg and Andersson 1982; Eriksson et al. 1983; Keller et al. 1990).

Trout predation probably accounted for the significantly lower density of macroinvertebrates in the profundal habitat of Whitepine Lake in the final survey. Lake trout and yellow perch populations in Laundrie Lake were probably of similar size throughout the interval between benthic surveys; catch per unit effort for stocked trout was 0.39·100 metre-hours^{-1} (gill nets) in 1982 and 0.29 in 1988, while that for perch was 43.4·day^{-1} (trap net) in 1982 and 20.0 in 1988 (J. M. Gunn, Ontario Ministry of Natural Resources, Sudbury, Ont., unpubl. data). In contrast, the lake trout population in Whitepine Lake increased sharply from 1981 to 1987, while the perch population steeply declined (Gunn and Keller 1990).

Analysis of stomach contents (Table 7) suggests that the diet and feeding niche of these fishes overlap. The occurrence of dipteran pupae and terrestrial insects in the stomachs of both species indicates that they both feed near or at the surface. Similarly, both species feed in the limnetic habitat as shown by the occurrence of *Chaoborus*, adult aquatic bugs and beetles, fish remains (larger individuals), and cladocerans (smaller individuals). Furthermore, both species utilized the littoral habitat as shown by the occurrence of benthic macroinvertebrates such as alderflies, caddisflies, mayflies, dragonflies, and crayfish.

The main difference in the diet and feeding niche of these fishes was indicated by benthic dipterans. Yellow perch consumed small-bodied dipterans that included ceratopogonids, tanytarsinids, orthoclads, and early instars of *Microtendipes, Sergentia*, and *Procladius*, a fauna that is more characteristic of the littoral habitat. Lake trout, meanwhile, consumed large-bodied chironomids that included *Chironomus, Sergentia, Microtendipes, Protanypus*, and *Procladius*, a fauna that is more characteristic of the profundal habitat.

The shift in Whitepine Lake from a yellow perch to a lake trout dominated fish community, therefore, suggests that fish predation shifted more into the profundal habitat and more onto large-bodied dipterans. The lower density of *Chironomus* and *Sergentia* in the final survey and lack of change in the density of *C. punctipennis* thus probably resulted from the higher predation pressure by trout and the limited refuge area from predation, i.e. that region of the hypolimnion with low dissolved oxygen concentrations. Fish predation has been shown to reduce populations of limnetic insects (Henrikson and Oscarson 1978; Eriksson et al. 1980; Hultberg and Andersson 1982; Evans 1989), although its effect on soft-sediment benthic fauna is unclear (Thorp 1986). Since at least *Chaoborus* and *Sergentia* undergo diel migrations through the limnion (Hamilton 1965; Roth 1968), these taxa may be more vulnerable to fish predation than nonmigratory benthic taxa. Thus, had trout not been present, the density of these invertebrates may have increased as observed in Laundrie Lake, a conclusion similarly noted by Eriksson et al. (1983) for European lakes.

Changes in the macroinvertebrate fauna of Bowland Lake, located just upstream of Laundrie Lake (Fig. 1), following neutralization and lake trout stocking (Keller et al. 1990; BAR Environmental 1992) parallelled many of those in Whitepine and Laundrie lakes (Table 8). The addition of powdered limestone in 1983 increased the pH from about 5.0 to 6.9; the pH then declined from 6.9 to about 5.5 from 1983 to 1989 (table 1 in Keller et al. 1992). The number of macroinvertebrate taxa in the littoral habitat increased after neutralization from 31 in 1982 to 52 in 1989. Several acid-sensitive taxa, e.g. *A. lomondi, Slavinia appendiculata, S. lacustris, Cladotanytarsus, Stempellinella*, and *Amnicola*, were among the invading

TABLE 7. Aquatic macroinvertebrate taxa found in the stomachs of lake trout and yellow perch. Fish were sampled from Whitepine Lake in May and October 1981 and June and August 1987, from Laundrie Lake in September, and from Bowland Lake in May, July, and October.

		Lake trout				Yellow perch	
		Whitepine					
Feeding niche	Prey taxa	1981	1987	Laundrie 1988	Bowland 1988	Laundrie 1988	Bowland 1988
Surface	True flies						
	Chaoborus pupa		*	*	*		
	Chironomid pupa	*	*	*	*	*	*
Limnetic	Bugs						
	Notonecta		*		*		*
	Corixidae		*		*		
	Hesperocorixa				*		
	Sigara				*		
	Beetles						
	Dubiraphia		*				
	Gyrinidae	*			*		
	Dytiscidae	*	*		*		
	Halipus		*		*		
	Hydroporus				*		
	True flies						
	Chaoborus		*	*	*	*	*
Benthic	Alderflies						
	Sialis	*	*		*		*
	Beetles						
	Dytiscidae	*			*		*
	Gyrinus				*		
	Caddisflies						
	Phryganea		*				
	Agrypnia	*	*	*	*	*	*
	Oecetis						*
	Limnephilidae						*
	Molanna				*		
	Neureclipsis					*	
	Polycentropus	*	*	*	*	*	*
	Phylocentropus		*	*	*	*	*
	Damselflies						*
	Dragonflies		*				
	Aeshna						*
	Boyeria						*
	Somatochlora					*	*
	Tetragoneuria					*	*
	Cordulia						*
	Ladona julia				*	*	*
	Leucorrhinia		*		*	*	*
	Gomphidae					*	
	Mayflies						
	Hexagenia	*	*				
	Caenis						*
	Eurylophella						*
	Leptophlebiidae	*			*		*
	True flies						
	Ceratopogonidae					*	*
	Chironomidae	*					
	Chironomus		*	*	*		
	Cladopelma					*	
	Cladotanytarsus						*
	Cryptochironomus				*		*
	Dicrotendipes						*
	Glyptotendipes				*		
	Micropsectra					*	*

TABLE 7. (*Concluded*)

Feeding niche	Prey taxa	Lake trout: Whitepine 1981	Lake trout: Whitepine 1987	Lake trout: Laundrie 1988	Lake trout: Bowland 1988	Yellow perch: Laundrie 1988	Yellow perch: Bowland 1988
Benthic	*Microtendipes*		*		*	*	*
	Pagastiella						*
	Parachironomus						*
	Paratanytarsus						*
	Polypedilum						*
	Nilothauma						*
	Sergentia		*	*	*	*	
	Tanytarsus				*	*	*
	Pseudochironomus						*
	Corynoneura						*
	Cricotopus						*
	Heterotrissocladius				*		*
	Mesopsectrocladius					*	*
	Monopsectrocladius					*	*
	Psectrocladius						*
	Zalutschia				*	*	*
	Protanypus		*		*		
	Ablabesmyia			*	*		*
	Conchapelopia				*		
	Procladius		*		*	*	*
	Crayfishes		*		*	*	*
	Clams						
	Sphaeriidae		*				

TABLE 8. Change in pH, fish abundance, and density and number of taxa of benthic macroinvertebrates in Whitepine, Laundrie, and Bowland lakes between survey years. An up arrow indicates an increase between survey years, a down arrow indicates a decrease between survey years, and an equal sign indicates no change between survey years.

Lake	pH	Time period (yr)	Fish abundance	Littoral benthos: No. of taxa	Littoral benthos: Density	Profundal benthos: No. of taxa	Profundal benthos: Density
Whitepine	5.7–6.0	6	Perch ↓ Trout ↑	↑	↑	↑ or =	↓
Laundrie, northern basin	4.9–5.6	12	Perch = Trout =	↑	↑	↑	↑
Laundrie, southern basin	5.1–6.0	12	Perch = Trout =	↑	↑	↑ or =	↑
Bowland	5.2–6.9–5.5	7	Perch = Trout ↑	↑	=	↑	↓

species. Macroinvertebrate density, however, declined after neutralization from 9800·m^{-2} in 1982 to 6200·m^{-2} in 1984, but by 1989, it was again similar to that found in 1982. The number of taxa in the profundal habitat of Bowland Lake also increased after neutralization from 10 in 1982 to 16 in 1989. Density of profundal macroinvertebrates declined from about 18 000·m^{-2} in 1982 to 3500·m^{-2} in 1989. *Chaoborus, Sergentia,* and *Chironomus* were largely responsible for this decline.

A decrease in the littoral density of macroinvertebrates immediately following neutralization is generally observed in whole-lake experiments (Scheider et al. 1975; Hultberg and Andersson 1982; Eriksson et al. 1983; Raddum et al. 1984). This short-term response is at least partially an artifact of the manipulation (i.e. chemical shock). The lack of a change in the density of littoral macroinvertebrates 6 yr after neutralization, however, was the single response that differed markedly from that noted in Whitepine and Laundrie lakes. This difference in the response of littoral macroinvertebrates suggests that neutralization may not completely reflect the ecosystem dynamics resulting from a reduction in acid emissions.

Trout predation was probably responsible for the reduced density of profundal macroinvertebrates in Bowland Lake as noted for Whitepine Lake; trout density increased greatly from 1982 to 1989, and their diet included those large-bodied dipterans that predominated the profundal fauna of the lake (Table 7).

Increased survival through reduced chemical toxicity appears to account for the greater number of taxa and higher density of macroinvertebrates. While the density of acid-tolerant species appears to increase as acidity is reduced, species richness appears not to increase until pH exceeds 5.5–5.8. Species richness in the littoral habitat of Whitepine Lake (4.1–5.6 taxa per sample) was similar to that in Laundrie Lake (4.9–5.7),

although the pH in the lake basins varied from 4.8 to 5.7. Schindler (1988) similarly noted that the chironomid fauna had not changed in an experimentally acidified lake that was allowed to recover from pH 5.0 to 5.5. Trout predation, however, may compensate for (e.g. *Chaoborus*) or exceed (e.g. *Chironomus, Sergentia*) the increase in survival rate afforded by reduced acidic conditions for some profundal macroinvertebrates, especially when the refuge area from predation is small. It is also possible that trout predation may improve the survival of some littoral invertebrates (e.g. *Paratanytarsus, Chironomus, L. variegatus, Pseudochironomus*) indirectly by reducing yellow perch numbers.

Reduced acidity also may indirectly improve the survival of macroinvertebrates by enhancing their food supply. The reduced Secchi depth in Whitepine and Laundrie lakes (Table 1) and Bowland Lake (BAR Environmental 1992) suggests that secondary productivity was augmented with detrital carbon, as algal biovolume appeared not to change during the interval between surveys (table 2 in Nicholls et al. 1992). The higher density of tanytarsini and lower density of *Heterotrissocladius* also suggest an increase in lake trophy (Saether 1979). The increased density of *C. punctipennis* and *C. flavicans* in Laundrie Lake, in particular, infers that the production of zooplankton prey increased with the reduction in acidity, since *Chaoborus* abundance is more a consequence of prey abundance and fish predation than lake chemistry (Northcote et al. 1978; Neill and Peacock 1980; Eriksson et al. 1983; Yan et al. 1985).

Biological recovery of industrially acidified lakes is possible solely by reducing emissions, provided that recolonizing species are not locally extinct. Littoral macroinvertebrates appear most responsive to changes in chemical conditions, while profundal macroinvertebrates also respond to changes in lake trout abundance.

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References

BAR Environmental. 1992. Experimental lake neutralization 1981–1990 technical report. Prepared for the Ontario Ministries of the Environment and Natural Resources. Volume 1: Methods and results. Sudbury, Ont.

Carpenter, S. R. 1990. Large-scale perturbations: opportunities for innovation. Ecology 71: 2038–2043.

Dermott, R. M. 1985. Benthic fauna in a series of lakes displaying a gradient of pH. Hydrobiologia 128: 31–38.

Dermott, R. M., J. R. M. Kelso, and A. Douglas. 1986. The benthic fauna of 41 acid sensitive headwater lakes in north central Ontario. Water Air Soil Pollut. 28: 283–292.

Eriksson, M. O. G., L. Henrikson, B. I. Nilsson, G. Nyman, H. G. Oscarson, A. E. Stenson, and K. Larsson. 1980. Predator–prey relations important for the biotic changes in acidified lakes. Ambio 9: 248–249.

Eriksson, F., E. Hornstrom, P. Mossberg, and P. Nyberg. 1983. Ecological effects of lime treatment of acidified lakes and rivers in Sweden. Hydrobiologia 101: 145–164.

Evans, R. A. 1989. Response of limnetic insect populations of two acidic, fishless lakes to liming and brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 46: 342–351.

Gunn, J. M., and W. Keller. 1984. Spawning site water chemistry and lake trout (*Salvelinus namaycush*) sac fry survival during spring snowmelt. Can. J. Fish. Aquat. Sci. 41: 319–329.

1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Tran. Am. Fish. Soc. 110: 669–707.

Hamilton, A. L. 1965. An analysis of a freshwater benthic community with special reference to the Chironomidae. Ph.D. thesis, University of British Columbia, Vancouver, B.C.

Henrikson, L., and H. G. Oscarson. 1978. Fish predation limiting the abundance of *Glaenocorisa p. propinqua* (Hemiptera). Oikos 31: 102–105.

Hultberg, H., and I. B. Andersson. 1982. Liming of acidified lakes: induced long-term changes. Water Air Soil Pollut. 18: 311–331.

Johnson, M. G., and O. C. McNeil. 1988. Fossil midge associations in relation to trophic and acidic state of the Turkey Lakes. Can. J. Fish. Aquat. Sci. 45(Suppl. 1): 136–144.

Keller, W., L. A. Molot, R. W. Griffiths, and N. D. Yan. 1990. Changes in the zoobenthos community of acidified Bowland Lake after whole-lake neutralization and lake trout (*Salvelinus namaycush*) reintroduction. Can. J. Fish. Aquat. Sci. 47: 440–445.

Keller, W., and J. R. Pitblado. 1985. Water quality changes in Sudbury area lakes, 1974–76 to 1981–83. Acidic Precipitation in Ontario Study Report No. 007/85. Ontario Ministry of the Environment, Toronto, Ont. 28 p.

1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

Keller, W., and N. D. Yan. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

Keller, W., N. D. Yan, T. Howell, L. A. Molot, and W. D. Taylor. 1992. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 52–62.

Kelso, J. R. M., and J. M. Gunn. 1984. Responses of fish communities to acidic waters in Ontario, p. 105–115. *In* G. R. Hendry [ed.] Early biotic responses to advancing lake acidification. Acid Precipitation Series. Vol. 6. Butterworth Publishers, Boston, MA.

LaZerte, B. D., and P. J. Dillon. 1984. Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario. Can. J. Fish. Aquat. Sci. 41: 1664–1677.

Mossberg, P., and P. Nyberg. 1979. Bottom fauna of small acid forest lakes. Inst. Freshwater Res. Drottningholm Rep. 58: 77–87.

Neill, W. E., and A. Peacock. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes, p. 715–724. *In* W. C. Kerfoot [ed.] The evolution and ecology of zooplankton communities. University Press of New England, Hanover, NH.

Nicholls, K. H., L. Nakamoto, and W. Keller. 1992. Phytoplankton of Sudbury area lakes (Ontario) and relationships with acidification status. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 40–51.

Northcote, T. G., C. J. Walters, and J. M. B. Hume. 1978. Initial impact of experimental fish introductions on the macrozooplankton of small oligotrophic lakes. Verh. Int. Ver. Limnol. 20: 2003–2012.

Raddum, G. G., G. Hagenlund, and G. A. Halvorsen. 1984. Effects of lime treatment on the benthos of Lake Sondre Boksjo. Inst. Freshwater Res. Drottningholm Rep. 16: 167–176.

Raddum, G. G., and O. A. Saether. 1981. Chironomid communities in Norwegian lakes with different degrees of acidification. Verh. Int. Ver. Limnol. 21: 399–405.

Roff, J. C., and R. E. Kwiatkowski. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

Roth, J. C. 1968. Benthic and limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera, Chaoboridae). Limnol. Oceanogr. 13: 242–249.

Saether, O. A. 1979. Chironomid communities as water quality indicators. Holarct. Ecol. 2: 65–74.

Scheider, W., J. Adamski, and M. Paylor. 1975. Reclamation of acidified lakes near Sudbury, Ontario. Ont. Min. Environ. Tech. Rep., Toronto, Ont. 129 p.

Schindler, D. W. 1988. Effects of acid rain on freshwater ecosystems. Science (Wash., DC) 239: 149–157.

Stephenson, M., and G. L. Mackie. 1986. Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca*. Can. J. Fish. Aquat. Sci. 43: 288–292.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos 47: 75–82.

Walker, I. R., C. H. Fernando, and C. G. Paterson. 1985. Associations of Chironomidae (Diptera) of shallow, acid, humic lakes and bog pools in Atlantic Canada, and a comparison with an earlier paleoecological investigation. Hydrobiologia 120: 11–22.

Wiederholm, T., and L. Eriksson. 1977. Benthos of an acid lake. Oikos 29: 261–267.

Wilkinson, L. 1987. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, IL.

Yan, N. D., R. W. Nero, W. Keller, and D. C. Lasenby. 1985. Are *Chaoborus* larvae more abundant in acidified than in non-acidified lakes in central Canada? Holarct. Ecol. 8: 93–99.

Effects of pH on Community Dynamics of Chironomidae in a Large River near Sudbury, Ontario

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Griffiths, R. W. 1992. Effects of pH on community dynamics of Chironomidae in a large river near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 76–86.

To identify the mechanism(s) by which acidity alters the composition and richness of chironomid communities and to determine the acid tolerance of chironomid taxa inhabiting a large river, pH was manipulated in three stream channels. The chironomid community that developed after a 10-wk exposure to pH 4.5 was poorer in species and lower in abundance than those exposed to pH 5.9 or 7.4 (reference pH). The reduced density of chironomids at pH 4.5 was not a result of differential egg deposition, behavioural drift, or emergence. Acid-enhanced larval mortality appeared to be the primary mechanism accounting for reduced density. *Tribelos* predomined in the channel acidified to pH 4.5, while *Ablabesmyia* was predominant in the other channels. *Tanytarsus, Microtendipes,* and *Nilothauma* were the most acid-sensitive taxa. When pH was returned to 7.4 from 4.5, the composition and density of the community changed rapidly; acid-sensitive species invaded quickly, and within 6 wk the community resembled that in the other channels. These results suggest that acidity is important in structuring and maintaining lotic communities and that reduction in acidic emissions should lead to rapid biological recovery of acidified lotic systems, provided that acid-sensitive species have survived in nearby refuges.

Nous avons modifié le pH de trois chenaux de rivières pour déterminer les mécanismes par lesquels l'acidité modifie la composition et la richesse des communautés de moucherons (Chironomidae) et pour évaluer la tolérance à l'acidité des taxons de Chironomidae rencontrés dans de grandes rivières. La communauté de moucherons qui s'est développée par suite d'une exposition de 10 sem à un pH de 4,5 comportait un nombre d'espèces et une abondance moins élevés que celles qui étaient exposées à un pH de 5,9 ou de 7,4 (pH de référence). La densité réduite de Chironomidae à un pH de 4,5 n'était imputable ni à des variations dans le schème de la ponte, ni à la dérive par suite de la sortie délibérée des sédiments, ni à la transition au stade adulte. Le principal mécanisme responsable de la diminution de densité se traduirait par la mortalité des larves due à l'accroissement de l'acidité. Le genre prédominant dans le chenal acidifié à 4,5 était *Tribelos*, comparativement à *Ablabesmyia* dans les autres chenaux. Les taxons les plus sensibles à l'acidité étaient *Tanytarsus, Microtendipes* et *Nilothauma*. Lorsque le pH a été ramené de 4,5 à 7,4, la composition et la densité de la communauté se sont modifiées rapidement; les espèces sensibles à l'acidité ont gagné du terrain rapidement, et dans les six semaines, cette communauté ressemblait à celles des autres chenaux. Ces résultats laissent penser que l'acidité constitue un facteur important dans la structuration et le maintien des communautés lotiques, et que la réduction des émissions acides devrait conduire à un rétablissement rapide de la biologie des écosystèmes lotiques acidifés, à la condition que les espèces sensibles à l'acidité aient survécu dans les refuges avoisinants.

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Many decades of acidic emissions from the smelting industry in Sudbury, Ontario, have elevated the acidity and metal concentrations in aquatic environments over a large area extending mainly northeast–southwest of Sudbury (Conroy et al. 1975; Jeffries 1984; Keller and Pitblado 1986). The adverse effects of reduced pH on biota of area lakes are well documented (e.g. Beamish and Harvey 1972; Roff and Kwiatkowski 1977; Yan 1979; Keller and Pitblado 1984; Kelso and Gunn 1984; MacIsaac et al. 1987). How acid deposition affects the biota of Sudbury streams and rivers, however, has received little attention.

The effects of reduced pH on many groups of stream biota, particularly crustaceans, molluscs, stoneflies, mayflies, and caddisflies, are well known (Haines 1981; Kimmel et al. 1985; MacKay and Kersey 1985; Simpson et al. 1985; Hall and Ide 1987; Smith et al. 1990), but those on chironomids are unclear. Chironomids appear to be equally abundant in acidic and non-acidic streams (Simpson 1983; MacKay and Kersey 1985). Yet, larval density (Allard and Moreau 1987) and adult emergence (Hall et al. 1980; Zischke et al. 1983) declined when pH was experimentally lowered, although no change in larval density was noted for short pulses of acid stress (Hopkins et al. 1989; Kratz et al. 1992). Chironomids are considered to be sensitive to acidity because of their drift response in acid-addition experiments (Hall et al. 1980; Bernard et al. 1990). No enhanced drift, however, was observed in the acid-addition experiments of Zischke et al. (1983), Ormerod et al. (1987), and Hopkins et al. (1989). Kratz et al. (1992) showed that acidity only enhanced chironomid drift in one of two experiments.

Chironomids are frequently the most abundant group of insects in aquatic environments and often account for at least half the species in macroinvertebrate communities (Coffman and Ferrington 1984; Pinder 1986; Berg and Hellenthal 1991). Only in a few acidification studies, however, have chironomid larvae been identified to genus, the level of taxonomic resolution typical for other macroinvertebrate groups. Simpson

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TABLE 1. Chemical characterization of water in the Vermilion River at the study site. Values show the range of three samples collected during the summer.

Variable	
Conductivity ($\mu mho \cdot cm^{-1}$)	65–79
Hardness ($mg \cdot L^{-1}$)	25–30
Calcium ($mg \cdot L^{-1}$)	7.1–8.5
Dissolved organic carbon ($mg \cdot L^{-1}$)	3.0–3.4
Alkalinity ($mg \cdot L^{-1}$)	16–24
Sulphate ($mg \cdot L^{-1}$)	10–12
Total phosphorus ($\mu g \cdot L^{-1}$)	4–8
Total Kjeldahl nitrogen ($\mu g \cdot L^{-1}$)	160–120
Total aluminum ($\mu g \cdot L^{-1}$)	15–36

(1983) noted that fewer chironomid taxa occurred in acidic streams (pH < 5) than in circumneutral streams (pH > 6) of the Adirondack Mountains, while Zischke et al. (1983) found that fewer chironomid taxa emerged from acidified stream channels (pH 6 and 5) than a reference channel (pH 8). In contrast, Allard and Moreau (1987) reported that the same Orthocladiinae and Chironomini taxa occurred in their reference (pH 6.5) and acidified (pH 4.0) channels.

The lack of taxonomic resolution also has affected the interpretation of chironomid sensitivity to acidity. Orthocladiinae are generally considered acid sensitive because their density is lower in acidic streams (MacKay and Kersey 1985) and their larval density (Allard and Moreau 1987) and adult emergence (Hall et al. 1980; Zischke et al. 1983) decline when pH is experimentally lowered. However, all six Orthocladiinae taxa reported by Allard and Moreau (1987) survived in the acidified stream channel (pH 4), while several "acid-tolerant" Chironomini taxa were not collected by Zischke et al. (1983) from their acidified channel (pH 5). Thus, each subfamily of Chironomidae is probably composed of acid-sensitive and acid-tolerant species. Taxa identified only to subfamily simply demonstrate the pattern of the most dominant species.

The purpose of my study was to determine the acid tolerance of chironomid taxa inhabiting a large river and to identify the mechanism(s) by which acidity alters species composition and richness. Several mechanisms may be important; acidity may inhibit egg deposition by females, increase mortality in larval or pupal stages through physiological stress, interfere with emergence, stimulate larval drift, alter food resources, and/or change biotic interactions. These mechanisms were investigated by observing changes in density of the different life-cycle stages (egg, larva, prepupa, pupa, adult) of chironomid taxa separately and combined in three stream channels. Previous field studies (Hall et al. 1980; Zischke et al. 1983; Allard and Moreau 1987; Ormerod et al. 1987) have examined the response of established macroinvertebrate communities to a severe depression of pH. In contrast, I examined the development of chironomid communities in stream channels lacking an established macroinvertebrate community under three levels of acidity (reference (pH 7.4), pH 5.9, pH 4.5) and then examined the response of the established chironomid communities in the acidified channels to pH recovery. The response of established lotic macroinvertebrate communities in acidic waters to an increase in pH has not been previously examined.

Methods

Study Site

The field site was located on the Vermilion River approximately 50 km north of Sudbury, Ontario, just east of the abandoned railway town of Milnet (46°49′N, 80°57′W). Mean width of the river was about 32 m; the substrate consisted of gravel and cobble, typical for a glaciofluvial outwash plain. The pH of the water was circumneutral (6.6–7.6) and no pronounced spring depression was noted in 1982 or 1983. In addition, the water was relatively soft, poor in nutrients, and low in ions (Table 1). The maximum summer water temperature was 25°C.

Experimental Design

Three plasticized plywood channels (8 m long, 0.5 m wide, 0.6 m high) were constructed side-by-side across a riffle near the centre of the river (Fig. 1) over a 3-d period. Hand-sorted gravel and cobble from nearby were placed throughout the channels, except in the first and last metre of each channel, to a depth of 8–10 cm. Water depth above the substrate was maintained at 12–18 cm by adjusting the length of a deflecting weir constructed upstream of the channels. Flow rate through the channels varied from 14 to 22 $L \cdot s^{-1}$.

Immediately after the channels were filled with substrate, pH in two of them was experimentally lowered for a 10-wk period from June 6 to August 15, 1982. Water flowing through the reference channel ranged from pH 7.0 to 7.6 (median 7.4) whereas water in the two acidified channels was maintained at pH 5.9 ± 0.3 (SD) and 4.5 ± 0.3 (Fig. 2) by continuously adding dilute H_2SO_4 (<0.5 M). H_2SO_4 was added from tanks positioned over the upstream end of each channel (Fig. 1). Each tank consisted of a 30-L plastic tub with a stainless steel cover, a float valve to maintain a constant volume of acid within the tub, and 10 separate delivery valves (syringes with detachable hypodermic needles) that, when opened, allowed acid to drip into the channel. A large float attached to the upstream end of each channel regulated the acid-addition rate as the water level fluctuated by changing the number of open delivery valves. Dilute acid was supplied by gravity flow to each tank via tygon tubing from separate 454-L nalgene storage tanks (Fig. 1), which held a 5- to 6-d supply of acid. To ensure thorough mixing, deflecting baffles were installed just downstream of the delivery valves.

On August 16, acid inputs to channels 2 and 3 ceased, and from then until September 26, the pH in all three channels varied from 7.4 to 7.6.

Macroinvertebrate Sampling

Benthos, drift, and emergence samples were collected from each channel from June 13 to September 26. Benthic invertebrates were sampled with a T-type sampler (0.05 m^2; 0.316-mm mesh) (Merritt and Cummins 1984). Samples were collected weekly for the first 4 wk, every other week until the end of the acid-addition period, weekly for the first 2 wk after acid-addition ceased, and every other week until the end of the study. On each sampling date, four benthic samples were collected from each stream channel. Sampling sites were located randomly and sampled only once during the study. All samples were preserved with 80% ethanol.

Drifting invertebrates were sampled with drift nets (125 × 400 mm aperture; 0.316-mm-mesh net) at the same frequency as benthos. Each of the two nets used in each channel filtered the entire water column (surface to substrate). They were positioned at the downstream end of each channel for a 24-h period and then at the upstream end of each channel for a 24-h period to sample drift exiting and entering each channel. The nets were emptied four to six times during a 24-h period. All samples were preserved with 80% ethanol.

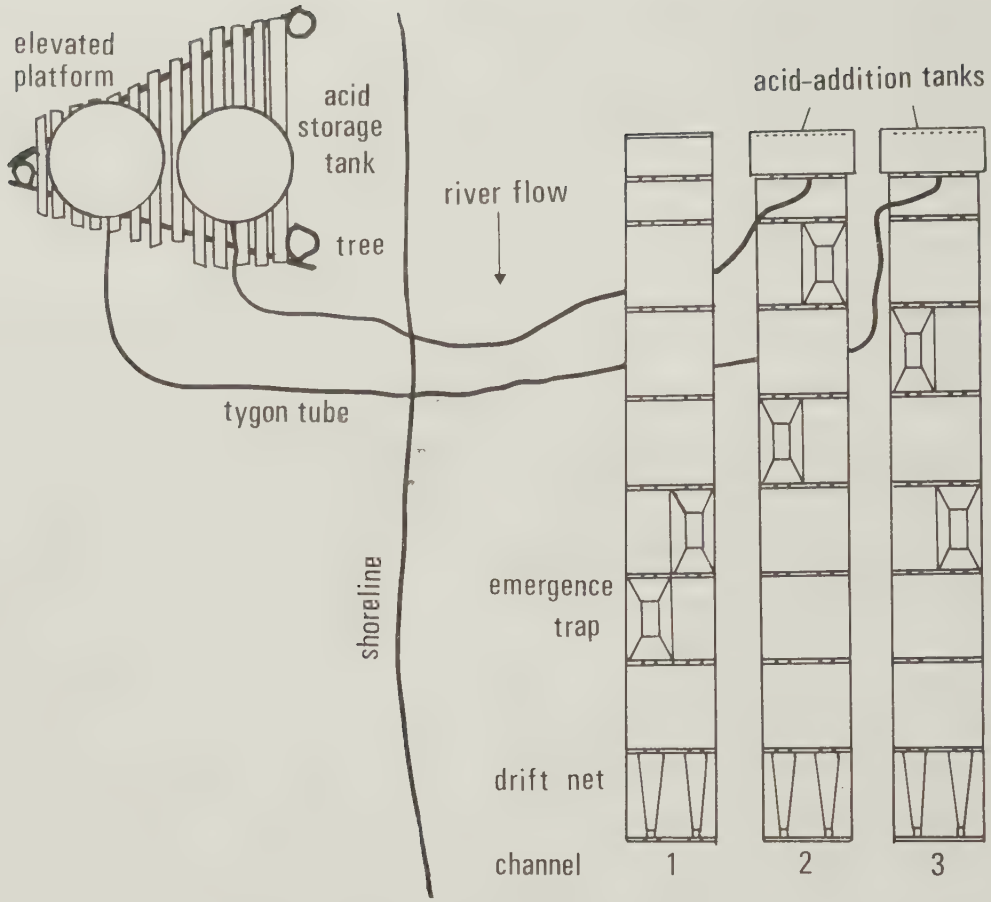

FIG. 1. Sketch of apparatus used in the field experiment.

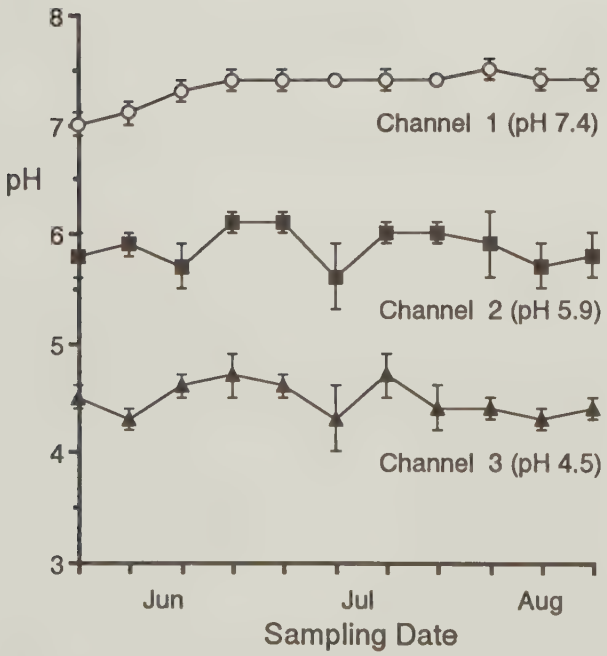

FIG. 2. pH (weekly median and range) in the three stream channels from June 6 to August 15, measured 1 m upstream from the end of the channels. Measurements were made three times per week. After August 15, pH in each channel varied from 7.4 to 7.6.

Floating traps (1 m long, 0.24 m wide, 0.5 m high) were used to collect emerging insects. Two traps per channel were randomly placed into 12 possible locations every week (Fig. 1). Emerging insects flew into a plastic collecting bottle attached to the top of the trap or fell onto a 16-cm-diameter funnel suspended within the trap and into an attached plastic collecting bottle. The collecting bottles were half filled with a 9:1 mixture of 80% ethanol and 10% ethylene glycol and were changed weekly.

Chironomid egg masses were removed and enumerated from benthic samples during the first 4 wk of the study to examine egg deposition rates. Chironomid larvae, prepupae (fourth instars with swollen thorax), and pupae with a head width >0.2 mm were removed and enumerated from benthic and drift samples. Larval chironomids were mounted on glass slides in a clearing medium (ACS) and identified to the generic level (Oliver and Roussel 1983; Wiederholm 1983). Adult chironomids were sorted and enumerated from the emergence samples.

Results

Colonization

Examination of drift entering the channels and egg-mass density indicated that colonization of the channels by chironomids was similar during the study. During the 10-wk acid-addition period, an average 72.6 ± 26.8 (SD), 94.0 ± 36.2, and 54.6 ± 19.4 chironomids·d^{-1} drifted into the reference channel and acidified channels 2 and 3, respectively.

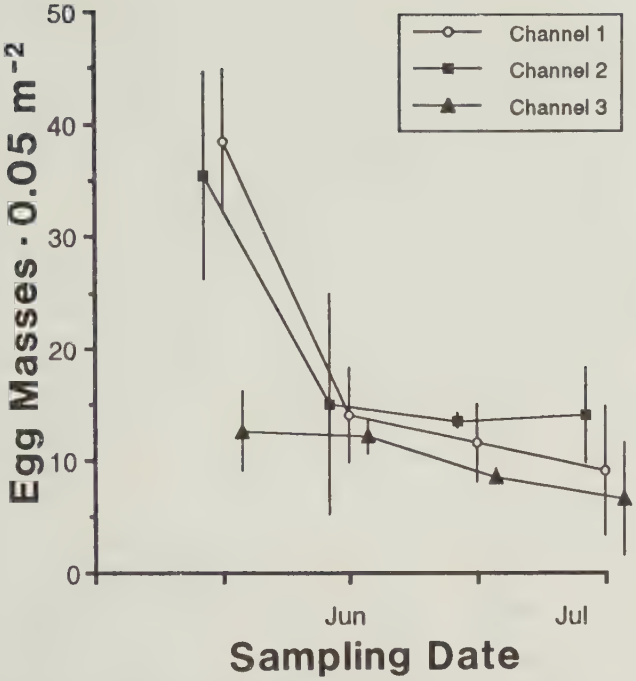

FIG. 3. Mean density of chironomid egg masses in the three stream channels from June 13 to July 4. pH in channels 1 (reference), 2, and 3 was 7.4, 5.9, and 4.5, respectively. Vertical lines represent 1 SD.

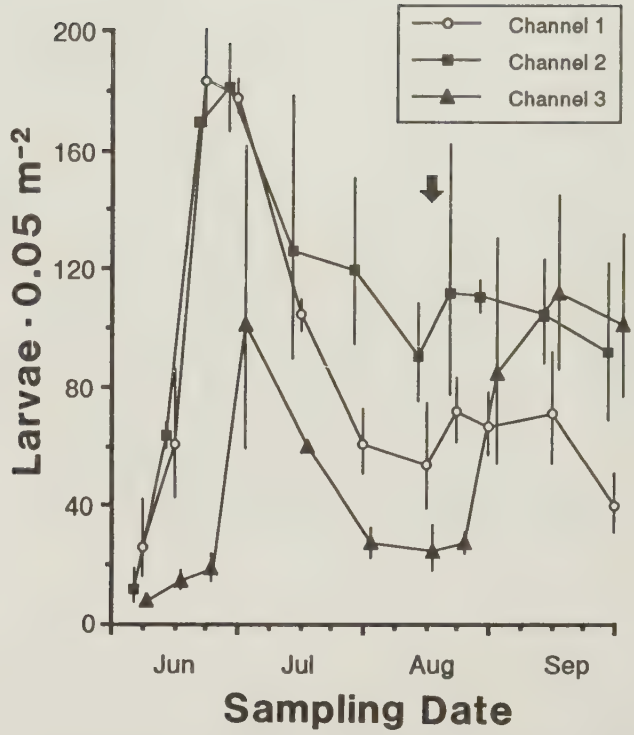

FIG. 4. Mean density of chironomid larvae in the three stream channels from June 13 to September 26. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. The arrow marks the end of the acid-addition period. pH in all channels after acid addition ceased was 7.4. Vertical lines represent 1 SD.

During the 6-wk post-acid-addition period, an average 30.0 ± 7.1, 50.0 ± 14.3, and 28.5 ± 9.3 chironomids·d^{-1} drifted into the channels, respectively. Assuming that drift samples collected at the upstream end of the channels represented a random temporal sampling, then the number of chironomids drifting into each of the acidification channels was not different from that drifting into the reference channel (Dunnett's test: $q' = 1.34$; $p > 0.05$, for both comparisons). The reduction in drift rate during the post-acid-addition period was at least partially a result of lower flow.

Egg-mass density also was similar among the channels over the initial 4 wk of the acid-addition period, except possibly on the first sampling date (Fig. 3). Ovipositing females thus appeared not to discriminate among channels because of pH.

Benthic Density

Larval density in each channel, which was near zero at the start of the study, increased exponentially during the first 3–4 wk and then declined to about half the maximum values until the end of the acid-addition period (Fig. 4). Throughout this period, larval density in channel 3 was always lower than that in the other channels. After the acid-addition period, larval density in the reference channel and channel 2 changed little whereas it rapidly increased in channel 3, reaching a maximum after 4 wk. Mean larval density in channel 3 was greater than that in the other channels during the last 2 wk of the study. Throughout the study, chironomid larvae typically accounted for more than 80% of the macroinvertebrates in each channel.

The density of prepupal chironomids also increased exponentially in each channel during the first 4 wk and then generally declined during the remainder of the acid-addition period (Fig. 5, upper panel). Throughout the acid-addition period, the density of prepupae in channel 3 was lower than that in the other channels, but it increased following the acid-addition period, reaching a density greater than that in the other channels after about 4 wk.

Similarly, pupal density in each of the channels increased exponentially during the first 4–6 wk and then declined during the remainder of the acid-addition period (Fig. 5, lower panel). Pupal density in channel 3 was always less than that observed in the other two channels. Following the acid-addition period, pupal density slowly declined in the reference channel and channel 2. However, the density of pupae in channel 3 peaked after 4 wk, again exceeding that in the other channels.

Over the acid-addition period, the mean densities of larvae, prepupae, and pupae in channel 3 were 42, 36, and 26% of those in the reference channel, respectively. This decline in life-stage abundance suggests a higher mortality rate in channel 3 than in the reference channel. During the acid-addition period, I noted that 12–18% of the chironomid larvae in channel 3 were covered with fungus whereas fungus-coated chironomids were not collected from the other channels or from channel 3 a week after the acid addition ceased. In the laboratory, I observed that heat-killed chironomid larvae placed in river water developed a fungus coating within 24 h. Thus, fungus-coated chironomids in the field samples probably represented dead individuals, again implying that the mortality rate was higher in channel 3.

Larval Composition

Twenty-six taxa were identified from the channels (Table 2). Ten taxa were sufficiently abundant over the study period to evaluate general population response patterns to pH (Tanypodinae: *Ablabesmyia*, *Labrundinia*, *Paramerina*, and *Conchapelopia*; Chironomini: *Microtendipes*, *Tribelos*, and *Nilothauma*; Tanytarsini: *Tanytarsus*; and Orthocladiinae: *Psectrocladius*, and *Heterotrissocladius*). The density of acid-

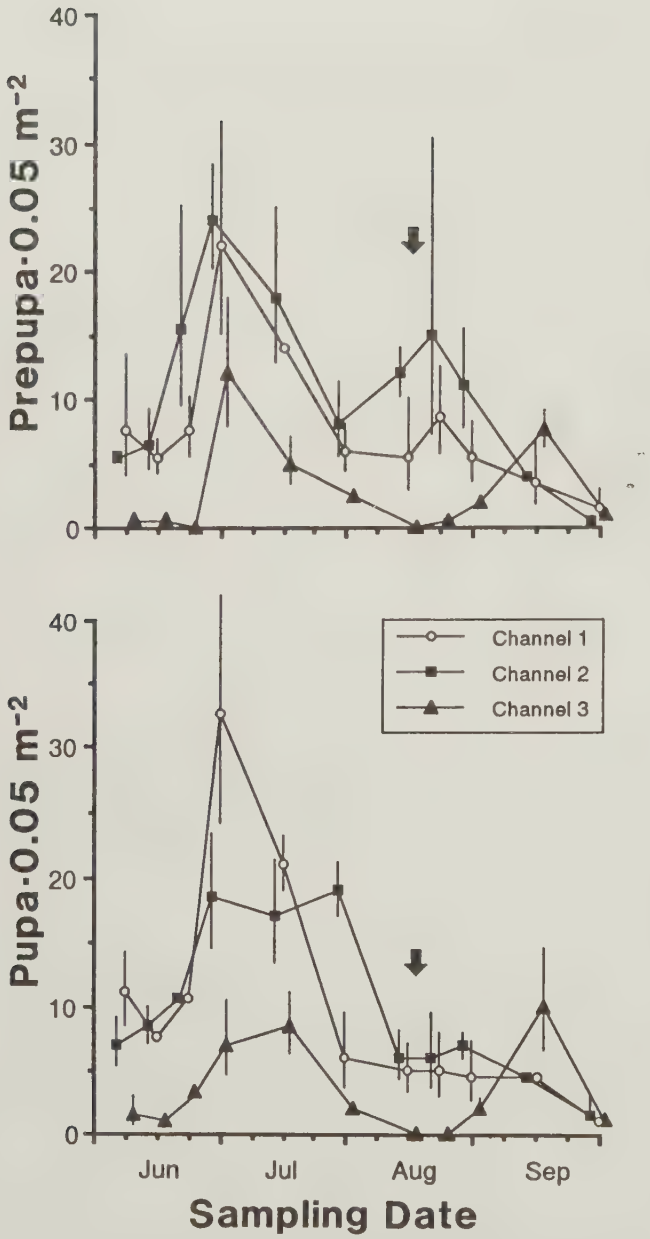

FIG. 5. Mean density of chironomid prepupae (upper panel) and pupae (lower panel) in the three stream channels from June 13 to September 26. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. The arrow marks the end of the acid-addition period. pH in all channels after acid addition ceased was 7.4. Vertical lines represent 1 SD.

sensitive taxa increased rapidly in the reference channel and channel 2 over the first 3–5 wk of the acid-addition period (Fig. 6). Their density in the reference channel then generally declined during the remainder of the acid-addition period whereas the density of some taxa in channel 2 did not decline but remained almost constant. The density of acid-sensitive taxa in channel 3, however, was almost always lower than that in the other two channels throughout the acid-addition period. After the acid-addition period, midge densities in channel 3 increased steadily, reaching values similar to those in the reference channel and channel 2 before the end of the study.

In contrast, *Psectrocladius* and *Tribelos* exhibited an acid-tolerant pattern; their mean densities were generally higher in the acidified channels than in the reference channel throughout the acid-addition period (Fig. 7).

The density of *Psectrocladius* in the acidified channels increased rapidly from the start of the study and reached a peak in 4–6 wk (Fig. 7). It then declined during the remainder of the acid-addition period; density in channel 2 generally exceeded that in channel 3. Density in the reference channel was always low and never exceeded three individuals per sample. Following the acid-addition period, densities in the reference channel and channel 2 peaked after 4 wk and then declined to zero. The density in channel 2 also declined to zero, but slowly over the 6-wk post-acid-addition period.

Tribelos appeared in the acidified channels earlier than in the reference channel (Fig. 7). Its density in the acidified channels remained generally higher than that in the reference channel even after the acid-addition period.

Community Structure and Composition

In early August, the structure and composition of the chironomid community that developed in channel 2 after 8-10 wk at pH 5.9 were similar to those in the reference channel (Fig. 8; Table 2). Species richness (number of taxa per sample), although higher (11.0), was not different (t-test; $p > 0.05$) from that in the reference channel (8.0); however, larval density in channel 2 (105 $\pm$ 1.35 (mean $\pm$ SD) individuals · 0.05 m^{-2}) was higher (t-test; $p < 0.05$) than that in the reference channel (57 $\pm$ 1.35). In the reference channel and channel 2, larvae of *Ablabesmyia* were predominant and together with *Labrundinia*, *Conchapelopia*, *Microtendipes*, and *Tanytarsus* accounted for more than 80 and 70% of the chironomids, respectively. The greater density of *Psectrocladius* and the occurrence of *Polypedilum*, *Dicrotendipes*, *Procladius*, *Cryptochironomus*, and *Cricotopus* largely distinguished the community in Channel 2 from that in the reference channel. These latter five taxa, however, accounted for just 9% of the chironomid fauna in channel 2.

The removal of pH stress caused little change in the chironomid composition of channel 2. In late September, after 4–6 wk of pH 7.4, it still resembled that in the reference channel (Fig. 8; Table 2). Species richness in the reference channel and channel 2 both declined to 6.3 taxa per sample, while chironomid density in the reference channel (55 $\pm$ 1.56 individuals · 0.05 m^{-2}) and channel 2 (98 $\pm$ 1.35) remained essentially the same as that observed in early August. *Ablabesmyia*, *Conchapelopia*, *Tanytarsus*, and *Microtendipes* composed 75–85% of the larvae in each channel, with *Conchapelopia* accounting for almost 50% of the chironomids.

The structure and composition of the chironomid community that developed in channel 3 after 8–10 wk at pH 4.5 differed from those in the reference channel (Fig. 8; Table 2). Species richness in channel 3 was lower than that in the reference channel. In addition, the coefficient of variation (CV) for species richness in channel 3 (60.9%) was three times that in the reference channel (20.0%), indicating that variability in the spatial and temporal distribution of species in channel 3 was much greater than in the reference channel. This greater variability precluded a statistical evaluation of the mean differences in species richness between channels. Larval density, however, was lower (t-test; $p < 0.05$) than that in the reference channel. Larvae of *Tribelos* alone accounted for more than 50% of the fauna. *Ablabesmyia*, *Labrundinia*, *Conchapelopia*, and *Tanytarsus* represented about 40% of the community and *Microtendipes* was not present.

TABLE 2. Density (individuals·0.05 m^{-2}) and relative abundance (%) of larval chironomids in three stream channels in early August, following 8–10 wk of acid addition, and in late September, 4–6 wk after acid-addition ceased. Data represent the mean of samples collected on two sampling dates in each time period. An asterisk indicates a mean density of less than 1 per sample.

	August						September					
	1 (ref.) pH 7.4		2 pH 5.9		3 pH 4.5		1 (ref.) pH 7.4		2 pH 7.4		3 pH 7.4	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Ablabesmyia	19	33	40	38	5	18	8	15	9	9	12	12
Tanytarsus	9	15	6	5	2	7	1	2	3	3	7	7
Microtendipes	8	14	3	3			7	12	24	25	37	35
Conchapelopia	8	14	18	17	1	5	27	49	46	47	22	21
Labrundinia	6	11	9	9	2	9						
Heterotrissocladius	2	4	1	1	1	4						
Paramerina	1	2	5	5								
Nilothauma	1	2	*	*			*	*	4	4	4	4
Tribelos	1	2	3	3	14	52	2	3	9	9	11	10
Psectrocladius	*	*	8	8	*	*	6	11	*	*	6	5
Polypedilum fallax	*	*	1	1			*	*				
Rheocricotopus	*	*			*	*						
Eukiefferiella	*	*					*	*				
Polypedilum			4	3			*	*				
Dicrotendipes			2	2							2	2
Procladius			2	2								
Cryptochironomus			1	1								
Cricotopus			1	1			2	3	1	1	2	2
Phaenopsectra			*	*								
Paratendipes							*	*				
Parachironomus							*	*				
Rheotanytarsus									1	1		
Stempellinella											1	1
Nanocladius											1	1
Larsia[a]												
Corynoneura[a]												

[a]Not collected during the times specified.

The removal of pH stress caused a marked change in the chironomid composition of channel 3. In late September, after 4–6 wk of pH 7.4, its structure and composition resembled those in the other channels (Fig. 8; Table 2). Species richness increased from 5.3 to 7.8, which was not different (ANOVA; $p > 0.05$) from that in the other two channels. The CV for species richness declined to 21.9%, a value similar to that in the other channels. Chironomid density in channel 3 increased about fourfold, from 26 $\pm$ 1.36 to 106 $\pm$ 1.36 individuals · 0.05 m^{-2}, to match that in channel 2. *Ablabesmyia*, *Conchapelopia*, *Tanytarsus*, and *Microtendipes* composed 75–85% of the larvae in the channel, with *Conchapelopia* and *Microtendipes* accounting for >50% of the chironomids.

Drift

At the end of the first week of acid addition, chironomid drift from channel 3 was 2.5 times that from the reference, while drift from channel 2 was 1.5 times that from the reference channel. This pattern, however, changed during the remainder of the acid-addition period. During the 10-wk acid-addition period, an average 81.4 ± 30.8 (SD), 114.4 ± 41.5, and 63.4 ± 47.1 chironomids · d^{-1} drifted from the reference channel and acidified channels 2 and 3, respectively. The CV for drift from channel 3 (74.3%) was about twice that of the other two channels, indicating that the variability in the temporal distribution of drift was much greater from channel 3 than from the others. During the 6-wk post-acid-addition period, an average 30.7 ± 5.0, 41.3 ± 16.2, and 28.7 ± 17.2 chironomids · d^{-1} drifted from the channels, respectively.

Drift rate and benthic density were positively related during and after the acid-addition period (Fig. 9), suggesting that acidity may indirectly affect drift through its effect on benthic chironomid density. The lower slope of the post-acid-addition relationship (Fig. 9B), which is about half that of the acid-additional relationship (Fig. 9A), probably reflects the lower flow of the river during that period because the drift rate entering the channels was also halved. The lower drift typically observed from channel 3 during the acid-addition period thus probably reflected the reduced benthic density of chironomids in the channel.

Emergence

Chironomids accounted for 94% of adult insects emerging from the three channels. Emergence of chironomids from the reference channel peaked after about 4–5 wk and then declined over the remainder of the study (Fig. 10). Chironomid emergence from channel 2 followed that from the reference channel for the first 4 wk, but peaked after 6–7 wk and thereafter declined. Thus, peak emergence from channel 2 was delayed by 3 wk. Emergence from channel 3 increased steadily from the beginning of the study, peaked after about 6 wk, and then declined during the remainder of the acid-addition period. During the acid-addition period, emergence was lower from channel 3 on all dates compared with either of the other channels. During this 10-wk period, 491 $\pm$ 1.16 chironomids ·

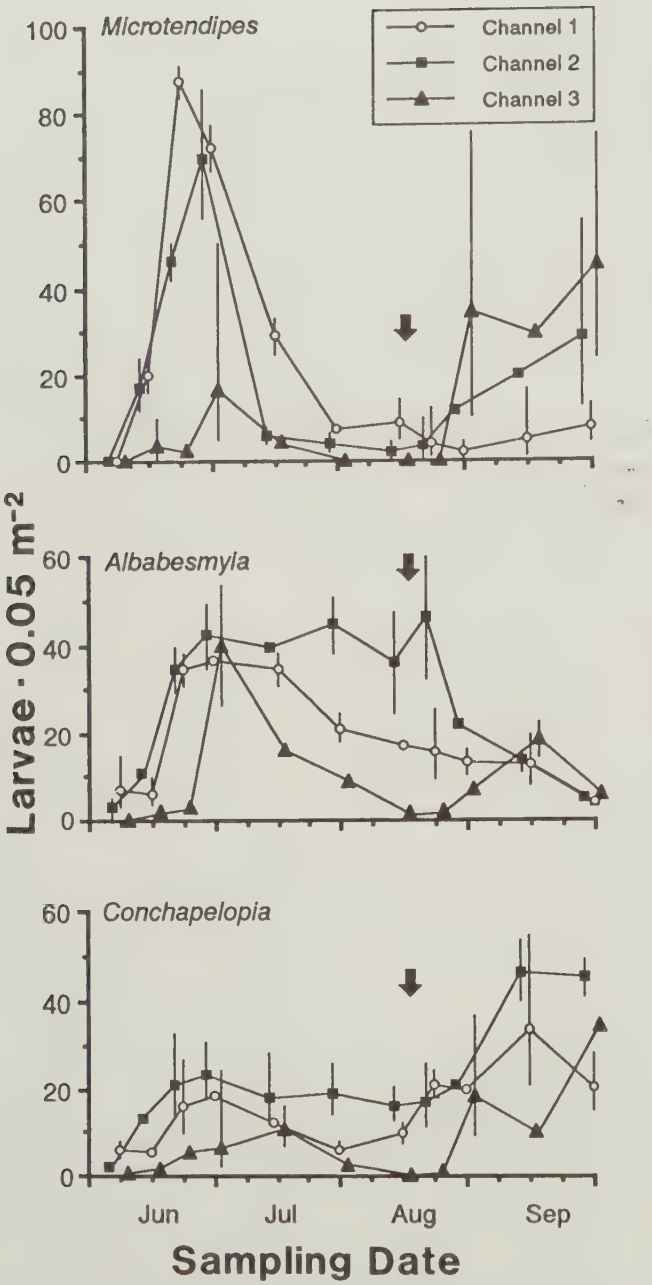

FIG. 6. Mean density of *Microtendipes*, *Ablabesmyia*, and *Conchapelopia*, examples of acid-sensitive chironomids, in the three stream channels from June 13 to September 26. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. The arrow marks the end of the acid-addition period. pH in all channels after acid addition ceased was 7.4. Vertical lines represent 1 SD.

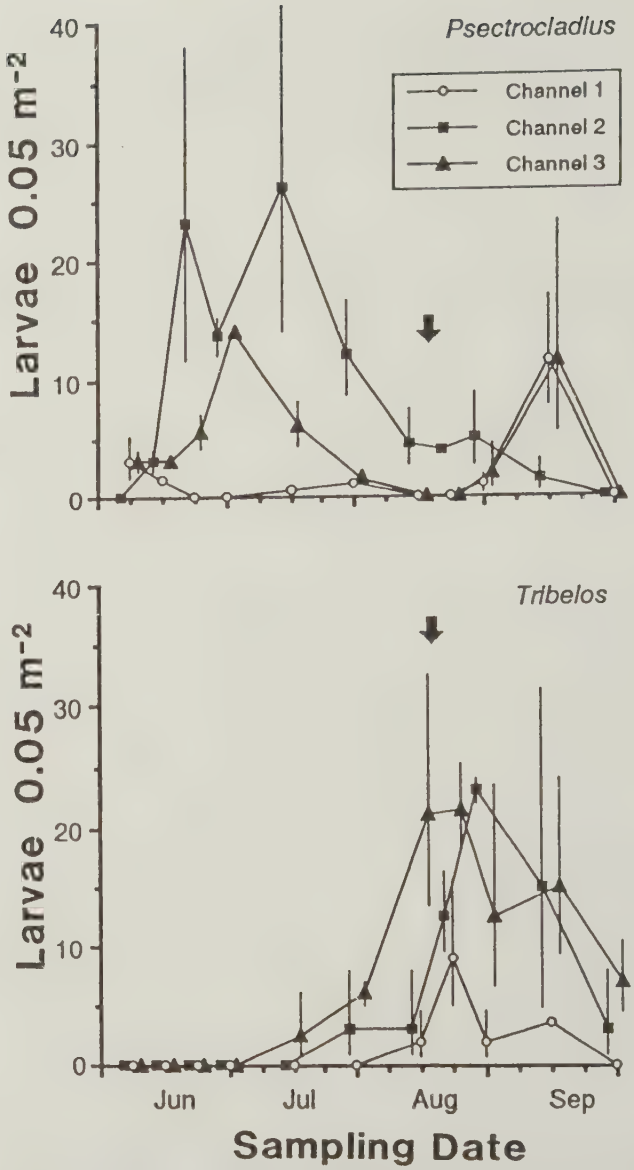

FIG. 7. Mean density of *Psectrocladius* and *Tribelos*, examples of acid-tolerant chironomids, in the three stream channels from June 13 to September 26. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. The arrow marks the end of the acid-addition period. pH in all channels after acid addition ceased was 7.4. Vertical lines represent 1 SD.

0.25 m^{-2} were collected from channel 3 compared with 2184 ⁄ 1.21 and 2013 ⁄ 1.34 from from channel 2 and the reference channel, respectively. However, emergence increased from channel 3 following the acid-addition period; on the last sampling date, mean emergence from channel 3 was greater than that from the other two channels.

An estimate of the daily number of pupae that developed into adults was calculated for each channel by regressing daily emergence (weekly emergences divided by 7) for each week onto the pupal density at the beginning of the week. An ANCOVA indicated that the slopes of the three regressions (Table 3) were not different ($p > 0.80$); in fact, the three regressions were coincident ($p > 0.20$). This suggests that approximately 30% (common slope) of pupae developed into adults each day, independent of pH. Similarly, an ANCOVA indicated that the proportion of pupae developing into adults per day following the acid-addition period (Table 3) was not different ($p > 0.85$) from that during the acid-addition period.

Discussion

Tolerance of Chironomid Taxa to Acidity

Field surveys have shown that lotic chironomids occur in moderately acidic conditions, i.e. pH 5–6 (MacKay and Kersey 1985; Smith et al. 1990). In my study, chironomid taxa generally tolerated the reduction in pH from 7.4 to 5.9; the density and relative abundance (percent) of four Tanypodinae, six Chironominae, and two Orthocladiinae taxa exposed to pH 5.9 were equal or greater than those under reference

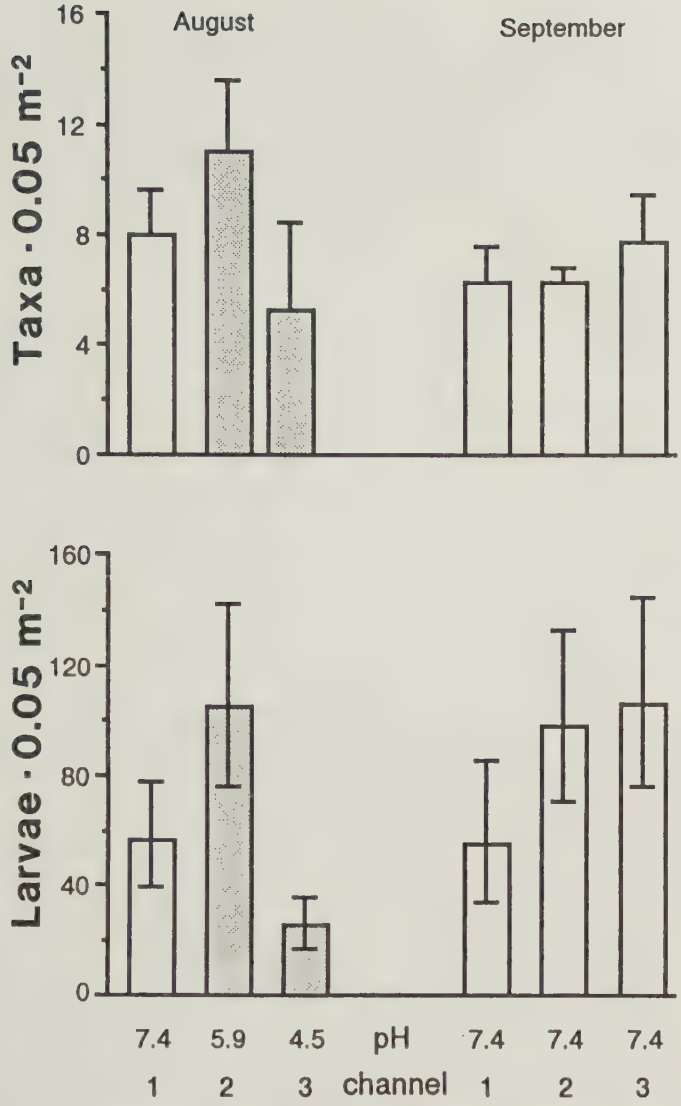

FIG. 8. Mean species richness and density of larval chironomids in the reference (channel 1) and acidified channels (channels 2 and 3) in early August, after 8–10 wk of acid addition, and in late September, 4–6 wk after acid addition ceased. Vertical lines represent 1 SD.

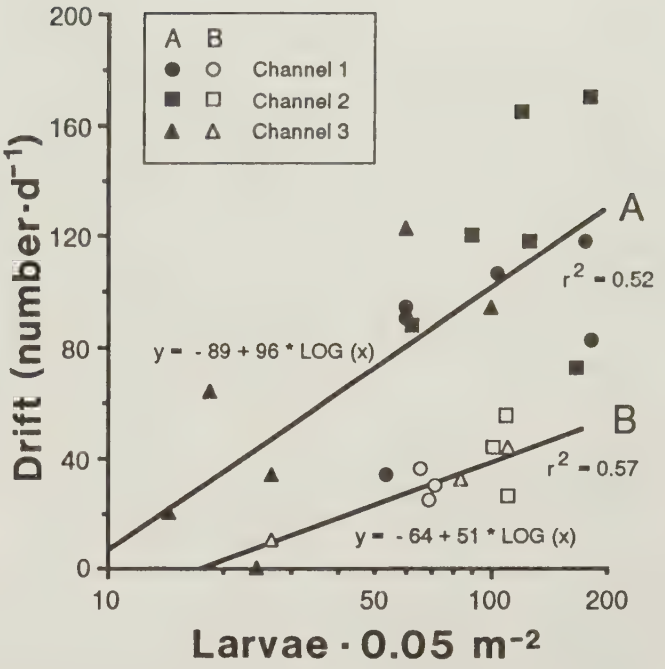

FIG. 9. Relationship between chironomid drift rate and benthic density in the three stream channels (A) during and (B) after the acid-addition period. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. pH in all channels after acid addition ceased was 7.4.

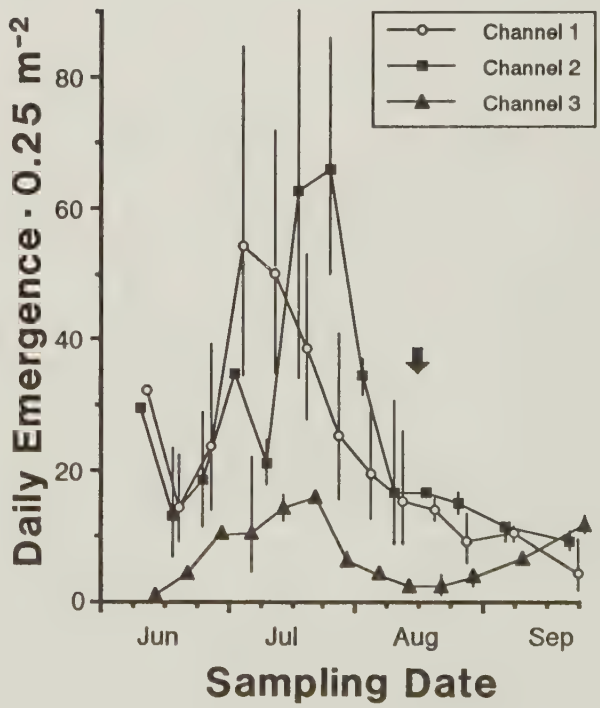

FIG. 10. Mean daily emergence of chironomids from the three stream channels from June 13 to September 26. During the 10-wk acid-addition period, pH was 7.4, 5.9, and 4.5 in channels 1 (reference), 2, and 3, respectively. The arrow marks the end of the acid-addition period. pH in all channels after acid addition ceased was 7.4. Vertical lines represent 1 SD.

conditions (Table 2). Increased drift during the initial week of acidification, however, suggests that some chironomids were sensitive to this pH reduction. Enhanced drift observed by Bernard et al. (1990) similarly showed that chironomids in a small British Columbian stream were sensitive to a pH reduction from 7.0 to 5.9. The lower density and relative abundance of *Tanytarsus*, *Microtendipes*, and *Nilothauma* after 8–10 wk of exposure to pH 5.9, and the subsequent increase in density and relative abundance of these taxa after the pH was returned to 7.4 from 5.9 (Table 2) indicate that they were the most acid-sensitive taxa. Individuals of these taxa thus possibly accounted for the short-term increase in drift.

Almost all chironomid taxa were intolerant of pH 4.5; except for *Tribelos*, the density and relative abundance of chironomid taxa exposed to pH 4.5 were lower than those under less acidic conditions (Table 2). *Tribelos* and *Psectrocladius* appeared most tolerant to pH 4.5 (Fig. 7), although whether they can maintain a population at this pH is unknown.

Lotic Orthocladiinae are typically considered to be more acid sensitive than Chironominae and Tanypodinae (Hall et al. 1980; MacKay and Kersey 1985; Allard and Moreau 1987). This

TABLE 3. Least-square regressions of daily chironomid emergence on pupal density for each stream channel and for all data combined. Data were analyzed separately for the acid-addition period (June 13 to August 15) and post-acid-addition period (August 16 to September 26). b = slope of regression; SE = standard error of the mean; n = number of observations; r^2 = coefficient of determination.

	Channel	pH	b	SE	n	r^2
Acid-addition period	1 (ref.)	7.4	0.27	0.03	13	0.89
	2	5.9	0.28	0.08	12	0.60
	3	4.5	0.28	0.03	13	0.76
	1, 2, 3		0.30	0.02	38	0.86
Post-acid-addition period	1, 2, 3	7.4	0.29	0.04	23	0.68

generalization, however, is based exclusively on studies conducted in small streams, where Orthocladiinae typically predominate (Pinder 1986; Berg and Hellenthal 1991). The most acid-sensitive taxa in the Vermilion River were the Chironominae *Tanytarsus*, *Microtendipes*, and *Nilothauma*. *Tanytarsus* from the Mississippi River was also found to be acid sensitive (Zischke et al. 1983), while *Microtendipes* from a small Canadian Shield stream was found to tolerate pH 4.0 (Allard and Moreau 1987). Generalizations about the acid tolerance of lotic chironomids at the subfamiliar or generic level thus may not be applicable, except on a regional or habitat basis.

Effect of Acidity on Chironomid Dynamics

After 8–10 wk of acidification, the density of benthic chironomids exposed to pH 5.9 was not less than that observed in the reference (pH 7.4) channel whereas the density of benthic chironomids exposed to pH 4.5 was significantly lower than that in the reference channel (Fig. 8). Allard and Moreau (1987) reported a similar decrease in density for chironomids exposed to pH 4.0. A reduction in density has frequently been found for lotic macroinvertebrates exposed to low-pH conditions (Fiance 1978; Arnold et al. 1981; Townsend et al. 1983; Zischke et al. 1983; Burton et al. 1985; Kimmel et al. 1985), even for short exposure periods (Herricks and Cairns 1974; Ormerod et al. 1987; Kratz et al. 1992), although the mechanisms are unclear.

Several mechanisms may account for the reduced density of benthic chironomids exposed to low pH. Sutcliffe and Carrick (1973) contended that the distribution of *Baetis* eggs in the River Duddon, England, resulted from acidity affecting site selection by ovipositing females. In my study, however, this mechanism was not evident; egg-mass density was similar in all stream channels regardless of pH (Fig. 3). But as shown by Rowe et al. (1988) for mayfly eggs, acidity may have reduced the hatching success of midges.

Increased acidity often causes an immediate, short-term increase in drift (Hall et al. 1980; Bernard et al. 1990; Kratz et al. 1992). This is sometimes sufficient to reduce the benthic density of some species (Ormerod et al. 1987; Kratz et al. 1992), although incoming drift may rapidly replenish the benthic population and mask this response (Hopkins et al. 1989). Increased drift was noted after the first week of exposure to pH 5.9 and 4.5. This probably reflected both a behavioural (i.e. chironomids actively entering the drift) and toxic (i.e. dead chironomids, whose death was a consequence of the acidity, passively entering the drift) response to reduced pH (Griffiths 1987; Hopkins et al. 1989; Kratz et al. 1992). During the remaining 9-wk acid-addition period, a single density-dependent relationship was observed between drift and benthic density irrespective of pH (Fig. 9A), suggesting that acidity had little direct effect on total drift. On a per capita basis, however, Fig. 9A indicates that the highest drift rate occurred at a benthic density of 22–24 chironomids · 0.05 m^{-2}, the same density that was observed in channel 3 after 8–10 wk of exposure to pH 4.5. For densities higher and lower than this, the drift rate per individual was lower. Acidity, therefore, probably accounted for the higher per capita drift rate of chironomids exposed to pH 4.5 relative to that of those exposed to pH 5.9 and 7.4.

Bell (1971) suggested that emergence was the critical life-cycle stage of insects affected by acidity. Hall et al. (1980) and Zischke et al. (1983) also concluded that the reduced density of adult insects emerging from their experimentally acidified lotic systems resulted from the effect of acidity on the emergence stage of the insects. Chironomid emergence, however, was not affected by pH 5.9 or 4.5; about 30% of pupae developed into adults per day from each stream channel, independent of pH (Table 3). Fiance (1978) and Burton et al. (1985) also found that acidity had little effect on the emergence of certain insect species. The reduced emergence observed by Hall et al. (1980) and Zischke et al. (1983), therefore, was probably just a consequence of the lower benthic insect density, as measured by Zischke et al. (1983) and implied by Hall et al. (1980), not a consequence of the effect of acidity on emergence.

Acidity kills many macroinvertebrates (Bell 1970, 1971; Havas and Hutchinson 1982; van Frankenhuyzen et al. 1985; Burton and Allan 1986; Hargeby and Petersen 1988), probably by disrupting physiological processes (Havas and Hutchinson 1983; Okland and Okland 1986; Willoughby and Mappin 1988). This mechanism is often cited to explain changes in invertebrate density (Fiance 1978; Hall et al. 1980; Zischke et al. 1983; Allard and Moreau 1987). The occurrence of dead, fungal-coated individuals and the more rapid decline in the density of consecutive life stages of chironomids when exposed to pH 4.5 indicate that acidity was similarly lethal to chironomid larvae at pH 4.5.

Acid-enhanced mortality, therefore, was probably the main mechanism that reduced the density of larval chironomids exposed to pH 4.5. Reduced hatching success of eggs, however, can not be ruled out as a contributing mechanism. Enhanced emergence and reduced egg deposition were unlikely mechanisms, while enhanced behavioural drift probably assisted in reducing chironomid density during the initial week of acidification.

The enhanced mortality of larval chironomids exposed to pH 4.5 appeared sufficient to reduce their density to near zero if incoming drift had been unavailable. Figure 9A indicates that all incoming drift settled into the benthos below a larval density of 8.5 individuals · 0.05 m^{-2}, while the number of chironomids settling from the drift exceeded that entering the drift between 8.5 and 22 individuals · 0.05 m^{-2}. The number of larvae settling from the drift equalled that entering the drift between 22 and 24 individuals · 0.05 m^{-2} whereas the number of larvae entering the drift exceeded that settling above a benthic density of 24 individuals · 0.05 m^{-2}. Thus, whenever the larval density was below 22–24 individuals · 0.05 m^{-2}, incoming drift supplemented the density of benthic larvae until this density was attained. This was virtually the mean benthic density noted for chironomids exposed to pH 4.5 for 8–10 wk, suggesting that had incoming drift been unavailable, the density of larvae would have approached zero. Since the density of

benthic larvae was not less than 22–24 individuals · 0.05 m^{-2}, pH 4.5 could not have been immediately lethal to drifting chironomids because they augmented the benthic community. Larvae thus tolerated this level of acidity, about 70% less than that used in other experimental studies (e.g. Hall et al. 1980; Allard and Moreau 1987), for several days before they died, an insufficient amount of time for most larvae to develop to the pupal stage, which appeared to be unaffected by low pH.

When pH was increased from 4.5 to 7.4, the density of chironomids increased quickly and within 4 wk was equal to or greater than that in the other channels. This rapid response occurred despite a lower incoming drift rate and no change in the proportion of pupae developing into adults. As benthic density increased, the per capita drift rate declined to about 20% of that noted at the end of the acid-addition period. The lack of dead, fungus-covered larvae 1 wk after pH returned to normal clearly indicated that the mortality rate was lower. This response, therefore, supports the previous conclusion that the lower density of chironomids exposed to pH 4.5 resulted from enhanced mortality caused by the acid treatment.

Effect of Acidity on Chironomid Composition

Simpson (1983) noted that acidic (pH 4.4–5.0) headwater streams in the Adirondack Mountains of New York had a different chironomid composition and lower species richness than near-neutral streams. Similarly, the chironomid community that developed after 8–10 wk of exposure to pH 4.5 was lower in species richness and differed in composition from that exposed to pH 7.4 (Table 2; Fig. 8). Acidity appears to directly alter chironomid composition and reduce species richness by sequentially eliminating taxa from the community through enhanced larval mortality. The high CV for species richness that was observed at pH 4.5 suggests that periodic recolonization attempts by acid-sensitive taxa were unsuccessful. A reduction in pH to just 5.9 appears sufficient to reduce larval density of some taxa (Table 2), while a reduction to 4.5 may eliminate all taxa typically found in large rivers.

Acidity may also indirectly alter chironomid composition and species richness through its effect on food resources and biotic interactions (Sutcliffe and Hildrew 1989). Acid-induced changes to food resources may account for the greater density of *Psectrocladius* and *Tribelos* that developed at pH 5.9 and 4.5 (Fig. 7). The biomass of diatoms, chlorophytes, and chrysophytes attached to rocks increased faster at pH 5.9 and 4.5 than at pH 7.4; on the last day of the acid-addition period, it was 80 and 100 times greater at pH 5.9 and 4.5 than at pH 7.4, respectively (Griffiths 1987). Similarly, the volume of detritus that accumulated at pH 5.9 and 4.5 always averaged about two to four times that at pH 7.4 (R. W. Griffiths, pers. obs.) The greater diversity and quantity of food resources may also explain the higher density of chironomids that occurred at pH 5.9 (Fig. 8) and the occurrence of chironomid taxa that were absent at pH 7.4 (Table 2). Acid-reduced competition and predation may have also contributed to the increased density of *Psectrocladius* and *Tribelos* at pH 4.5; however, it is unlikely that competition or predation was reduced at pH 5.9.

Acidity appears to be essential for maintaining the structure and composition of chironomid communities in acid waters. The chironomid community that developed at pH 4.5 quickly recovered when the pH was returned to normal. The density of acid-sensitive species rapidly increased within the community (Fig. 6), and in just 6 wk the community resembled that developed under less acidic conditions (Table 2). Biological interactions alone were not sufficient to maintain the community against the influx of invading species.

In summary, these results indicate that acidity is an important variable structuring lotic communities. It principally acts by sequentially filtering species from the community through enhanced larval mortality. Acidity may indirectly increase the density of acid-tolerant species by altering food resources. Because acidity is essential for the maintenance of communities in acid waters, a reduction in acid emissions should lead to a rapid biological recovery of acidifed lotic systems, as in lentic systems (Griffiths and Keller 1992), provided that extirpated acid-sensitive species still occur in nearby refuges.

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References

Allard, M., and G. Moreau. 1987. Effects of experimental acidification on a lotic invertebrate community. Hydrobiologia 144: 37–49.

Arnold, D. E., P. M. Bender, A. B. Hale, and R. W. Light. 1981. Studies on infertile, acidic Pennsylvania streams and their benthic communities, p. 15–33. *In* R. Singer [ed.] Effects of acidic precipitation on benthos. Proc. North American Benthological Society, Springfield, IL.

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Bell, H. L. 1970. Effects of pH on the life cycle of the midge *Tanytarsus dissimilis*. Can. Entomol. 102: 636–639.

1971. Effect of low pH on the survival and emergence of aquatic insects. Water Res. 5: 313–319.

Berg, M. B., and R. A. Hellenthal. 1991. Secondary production of Chironomidae (Diptera) in a north temperate stream. Fresh water Biol. 25: 497–505.

Bernard, D. P., W. E. Neill, and L. Rowe. 1990. Impact of mild experimental acidification on short term invertebrate drift in a sensitive British Columbia stream. Hydrobiologia 203: 63–72.

Burton, T. M., and J. W. Allan. 1986. Influence of pH, aluminum, and organic matter on stream invertebrates. Can. J. Fish. Aquat. Sci. 43: 1285–1289.

Burton, T. M., R. M. Stanford, and J. W. Allan. 1985. Acidification effects on stream biota and organic matter processing. Can. J. Fish. Aquat. Sci. 42: 669–675.

Coffman, W. P., and L. C. Ferrington Jr. 1984. Chironomidae, 551–652. *In* R. W. Merritt and K. W. Cummins [ed.] An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt Publ. Co., Dubuque, IA.

Conroy, N. I., K. Hawley, W. Keller, and C. Lafrance. 1976. Influences of the atmosphere on lakes in the Sudbury area. *In* Proc. First Spec. Symp. on atmospheric contribution to the chemistry of lake waters. J. Great Lakes Res. 2 (Suppl.): 146–165.

Fiance, S. B. 1978. Effects of pH on the biology and distribution of *Ephemerella funeralis* (Ephemeroptera). Oikos 31: 332–339.

Griffiths, R. W. 1987. Acidification as a model for the response of aquatic communities to stress. Ph.D. thesis, University of Waterloo, Waterloo, Ont. 110 p.

Griffiths, R. W., and W. Keller. 1992. Benthic macroinvertebrate changes in lakes near Sudbury, Ontario, following a reduction in acid emissions. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 63–75.

Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

Hall, R. J., and F. P. Ide. 1987. Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. Can. J. Fish. Aquat. Sci. 44: 1652–1657.

HALL, R. J., G. E. LIKENS, S. B. FIANCE, AND G. R. HENDRY. 1980. Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 61: 976–989.

HARGEBY, A., AND R. C. PETERSEN. 1989. Effects of low pH and humus on the survivorship, growth and feeding of *Gammarus pulex* (L.) (Amphipoda). Freshwater Biol. 19: 235–247.

HAVAS, M., AND T. C. HUTCHINSON. 1982. Aquatic invertebrates from the Smoking Hills, N.W.T.: effect of pH and metals on mortality. Can. J. Fish. Aquat. Sci. 39: 890–903.

1983. Effect of low pH on the chemical composition of aquatic invertebrates from tundra ponds at the Smoking Hills, N.W.T., Canada. Can. J. Zool. 61: 241–249.

HERRICKS, E. E., AND J. CAIRNS. 1974. The recovery of stream macrobenthos from low pH stress. Rev. Biol. (Lisb.) 10: 1–12.

HOPKINS, P. S., K. W. KRATZ, AND S. D. COOPER 1989. Effects of an experimental acid pulse on invertebrates in a high altitude Sierra Nevada stream. Hydrobiologia 171: 45–58.

JEFFRIES, D. S. 1984. Atmospheric deposition of pollutants in the Sudbury area, p. 118–154. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons, Inc., New York, NY.

KELLER, W., AND J. R. PITBLADO. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acidic deposition. Water Air Soil Pollut. 23: 271–291.

1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

KELSO, J. R. M., AND J. M. GUNN. 1984. Responses of fish communities to acidic waters in Ontario, p. 105–115. *In* G. R. Hendrey [ed.] Early biotic responses to advancing lake acidification. Acid Precipitation Series. Vol. 6. Butterworth Publishers, Boston, MA.

KIMMEL, W. G., D. J. MURPHEY, W. E. SHARPE, AND D. R. DEWALLE. 1985. Macroinvertebrate community structure and detritus processing rates in two southwestern Pennsylvania streams acidified by atmospheric deposition. Hydrobiologia 124: 97–102.

KRATZ, K. W., S. D. COOPER, M. R. WILLIAMS, AND J. M. MELACK. 1992. Effects of single and repeated experimental acid pulses on invertebrates in a high altitude Sierra Nevada stream. Freshwater Biol. (In press)

MACISAAC, H. J., T. C. HUTCHINSON, AND W. KELLER. 1987. Analysis of planktonic rotifer assemblages from Sudbury, Ontario, area lakes of varying chemical composition. Can. J. Fish. Aquat. Sci. 44: 1692–1701.

MACKAY, R. J., AND K. E. KERSEY. 1985. A preliminary study of aquatic insect communities and leaf decomposition in acid streams near Dorset, Ontario. Hydrobiologia 122: 3–11.

MERRITT, R. W., AND K. W. CUMMINS [ED] 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt Publ. Co., Dubuque, IA. 722 p.

OKLAND, J., AND K. A. OKLAND. 1986. The effects of acid deposition on benthic animals in lakes and streams. Experientia 42: 471–486.

OLIVER, D. R., AND M. E. ROUSSEL. 1983. The insects and arachnids of Canada, Part 11: The genera of larval midges of Canada. Agric. Can. Res. Branch Publ. 1746. Canadian Government Publishing Centre, Supplies and Services Canada, Ottawa, Ont. 263 p.

ORMEROD, S. J., P. BOOLE, C. P. MCCAHON, M. S. WEATHERLEY, K. PASCOE, AND R. W. EDWARDS. 1987. Short-term experimental acidification of a Welsh stream, comparing the biological effects of hydrogen ions and aluminum. Freshwater Biol. 19: 341–356.

PINDER, L. C. V. 1986. Biology of freshwater Chironimidae. Annu. Rev. Entomol. 31: 1–23.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

ROWE, L., J. HUDSON, AND M. BERRILL. 1988. Hatching success of mayfly eggs at low pH. Can. J. Fish. Aquat. Sci. 45: 1649–1652.

SIMPSON, K. W. 1983. Communities of Chironomidae (Diptera) from an acid-stressed headwater stream in the Adirondack Mountains, New York. Mem. Am. Entomol. Soc. 34: 315–327.

SIMPSON, K. W., R. W. BODE, AND J. R. COLQUHOUN. 1985. The macroinvertebrate fauna of an acid-stressed headwater stream system in the Adirondack Mountains, New York. Freshwater Biol. 15: 671–681.

SMITH, M. E., B. J. WYSKOWSKI, C. M. BROOKS, C. T. DRISCOLL, AND C. C. COSENTINI. 1990. Relationships between acidity and benthic invertebrates of low-order woodland streams in the Adirondack Mountains, New York. Can. J. Fish. Aquat. Sci. 47: 1318–1329.

SUTCLIFFE, D. W., AND T. R. CARRICK. 1973. Studies on the mountain streams of the English Lake District. I. pH, calcium and the distribution of invertebrates in the River Duddon. Freshwater Biol. 3: 437–462.

SUTCLIFFE, D. W., AND A. G. HILDREW. 1989. Invertebrate communities in acid streams, p. 13–29. *In* R. Morris, E. W. Taylor, D. J. A. Brown, and J.A. Brown [ed.] Acid toxicity and aquatic animals. Society of Experimental Biology. Seminar Series 34. Cambridge University Press, Cambridge, U.K.

TOWNSEND, C. R., A. G. HILDREW, AND J. FRANCIS. 1983. Community structure in some southern English streams: the influence of physicochemical factors. Freshwater Biol. 13: 521–544.

VAN FRANKENHUYZEN,K., G. H. GEEN, AND C. KOIVISTO. 1985. Direct and indirect effects of low pH on the transformation of detrital energy by the shredding caddisfly, *Clistoronia magnifica* (Banks) (Limnephilidae). Can. J. Zool. 63: 2298–2304.

WIEDERHOLM, T. [ED.] 1983. Chironomidae of the Holarctic region. Part 1: Larvae. Entomol. Scand. Suppl. 19.

WILLOUGHBY, L. G., AND R. G. MAPPIN. 1988. The distribution of *Ephemerella ignita* (Ephemeroptera) in streams: the role of pH and food resources. Freshwater Biol. 19: 145–155.

YAN, N. D. 1979. Phytoplankton community of an acidified, heavy metal-contaminated lake near Sudbury, Ontario: 1973–1977. Water Air Soil Pollut. 11: 43–55.

ZISCHKE, J. M., J. ARTHUR, K. NORDLIE, R. HERMANUTS, D. STUNDEN, AND T. HENRY. 1983. Acidification effects on macroinvertebrates and fathead minnow (*Pimephales promelas*) in outdoor experimental channels. Water Res. 17: 47–64.

Estimated Impacts of SO_2 Emissions from Sudbury Smelters on Ontario's Sportfish Populations

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Impacts of acidification on the major sportfish species in Ontario (lake trout (*Salvelinus namaycush*), brook trout (*S. fontinalis*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Stizostedion vitreum*)) were estimated from the results of extensive water quality surveys conducted during the period 1978–85. Local impacts, within the 17 000 km^2 area most affected by emissions from Sudbury smelters, were also estimated and compared with the provincial values. The estimated numbers of acidic lakes in Ontario in which viable sportfish populations have disappeared were 119 lake trout lakes (5.1% of known lake trout lakes), 34 brook trout lakes (1.6%), 52 smallmouth bass lakes (2.2%), and 14 walleye lakes (0.3%). Most of these affected lakes were in the Sudbury zone, where fish populations, paticularly those of lake trout, began declining more than 30 yr ago. The estimated numbers of critically acidic lakes in the Sudbury zone were 94 lake trout lakes, 14 brook trout lakes, 18 smallmouth bass lakes, and 7 walleye lakes. More recent sampling of a subset of Sudbury lakes indicated that substantial water quality improvements have occurred as a result of emission reductions from Sudbury smelters.

Les impacts de l'acidification sur les principales espèces de poisson gibier en Ontario (le touladi (*Salvelinus namaycush*), l'omble de fontaine (*S. fontinalis*), l'achigan à petite bouche (*Micropterus dolomieu*) et le doré (*Stizostedion vitreum*) ont été estimés à partir de résultats d'études approfondies de la qualité de l'eau réalisées entre 1978 et 1985. Les impacts locaux, à l'intérieur de la zone de 17 000 km^2 la plus touchée par les émissions des fonderies de Sudbury, ont également été estimés et ont été comparés aux valeurs au niveau provincial. Les nombres estimés de lacs acides en Ontario dans lesquels des populations viables de poisson gibier ont disparu étaient les suivants : 119 lacs à touladi (5,1% des lacs à touladi connus), 34 lacs à omble de fontaine (1,6%), 52 lacs à achigan à petite bouche (2,2%) et 14 lacs à dore (0,3%). La plupart de ces lacs touchés se trouvent dans les environs de Sudbury, où le déclin des populations de poisson, en particulier celles de touladi, a commencé il y a plus de 30 ans. Les nombre estimés de lacs dont l'acidité est critique dans la région de Sudbury étaient les suivants : 94 lacs à touladi, 14 lacs à omble de fontaine, 18 lacs à achigan à petite bouche et 7 lacs à doré. D'après les prélèvements les plus récents d'un sous-groupe de lacs de la région de Sudbury, on a enregistré une amélioration substantielle de la qualité de l'eau par suite des réductions des émissions des fonderies de Sudbury.

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More than 100 million tonnes of SO_2 and tens of thousands of tonnes of metal particulates have been released into the atmosphere during a century of mining and smelting of nickel- and copper-containing sulphide ores in the Sudbury, Ontario, area (OCTF 1982). The effects of industrial emissions on the biota of the Sudbury lakes have been the focus of much of the acidification-related research in Canada. In a recent review article, Kelso et al. (1990) indicated that with the exception of Atlantic salmon (*Salmo salar*) in Nova Scotia (Watt et al. 1983), the documented losses of fish populations in Canada, attributable to acidic deposition, have all occurred near Sudbury.

Losses of popular sportfish species, such as lake trout (*Salvelinus namaycush*), were first reported in lakes near (<30 km) the Sudbury smelters in the 1940s and 1950s (OWRC 1970; Kelso and Gunn 1984). In more remote areas (still within the Sudbury zone of effect), such as the La Cloche Mountains and the Temagami area, fish stock losses were generally not detected until the early 1960s (Harvey and Lee 1982; Kelso and Gunn 1984). The problem of lake acidification in the Sudbury area received widespread attention with the documentation of reproductive failure and extinction of various fish species in Lumsden Lake, George Lake, and other La Cloche Mountain lakes (Beamish and Harvey 1972; Beamish et al. 1975; Harvey 1975). The potential large-scale damage to aquatic resources posed by airborne emission from Sudbury smelters was further illustrated by the extinction (before 1968) of aurora trout (*S. fontinalis, timagamiensis*), a rare subspecies of brook trout (*S. fontinalis*), from all three of its native lakes after acidification occurred. These lakes are located approximatley 110 km to the northwest of the smelters (Keller 1978).

Most of the current models that use extensive survey data (e.g. Wales and Beggs 1986; Neary and Dillon 1988; Minns et al. 1990) to predict biological "damage" are based on the now well-established negative relationships between species richness (the number of species present) and acidity (also inorganic Al) (Matuszek and Beggs 1988; Minns 1989; Schindler

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FIG. 1. Sulphur deposition zones in Ontario, 1983 (from Neary et al. 1990). Data are in g $S \cdot m^{-2} \cdot yr^{-1}$.

et al. 1989; Minns et al. 1990). Species richness models and regional lake water quality models (e.g. Jones et al. 1990) can be combined to make predictions of damage to certain sensitive groups of aquatic organisms (fish, molluscs, algae, etc.) (Minns et al. 1990). However, it is difficult to predict resulting community composition or, more specifically, to estimate extent of damage to individual fish species using such models.

In our study, we took a more direct approach at estimating acidification impacts to fish species of interest. From extensive chemical and biological surveys, we collected information on the geographic distribution and chemical characteristics of lakes in Ontario that historically contained populations of the four major sportfish species: lake trout, brook trout, walleye (*Stizostedion vitreum*), and smallmouth bass (*Micropterus dolomieu*). Literature information on lethal thresholds was used to estimate the impact of acidification on individual sportfish populations. Losses due to emissions from Sudbury smelters were then compared with losses in areas remote from Sudbury. Additional surveys conducted on lake trout lakes in the Sudbury area during the years 1980, 1987, and 1990 were used to examine temporal trends in water quality and to assess the significance of observed water quality improvements that accompanied emission reductions from Sudbury smelters in recent decades (Dillon et al. 1986; Keller and Pitblado 1986; Gunn and Keller 1990; Keller et al. 1992b).

Methods

Acid deposition zones in Ontario (Fig. 1) were mapped by the Ontario Ministry of the Environment (MOE) based on the 1983 data from a network of deposition monitoring stations and the sampling of an extensive set of lakes ($n = 5982$) by MOE and the Ontario Ministry of Natural Resources (MNR) (Neary et al. 1990). The Sudbury zone, the zone in which lakes were affected primarily by local SO_2 emissions, was defined as the area in which the sulphur concentration in lake water exceeded expected values for Ontario (i.e. $SO_4 > 200$ $\mu eq \cdot L^{-1}$), and most of the alkalinity has been replaced by sulphate ($[SO_4]/([SO_4] + [Alk]) > 0.7$) (Neary et al. 1990). The Sudbury zone, so defined, has a surface area of 17 022 km^2 and contains 10 643 lakes (≥ 1 ha) with a combined surface area of 281 513 ha. (Neary et al. 1990).

Atlases of the distribution of major sportfish species in Ontario were constructed from the results of netting surveys of more than 10 000 Ontario lakes (Dodge et al. 1985) and from information provided by MNR personnel in district offices across the province. These atlases do not represent fish species presence at a particular point in time but rather a summary of accumulated knowledge. Excluding the Great Lakes and Lake St. Clair, the atlases indicate that lake trout have been found in 2318 lakes, brook trout in 2110 lakes, smallmouth bass in 2416

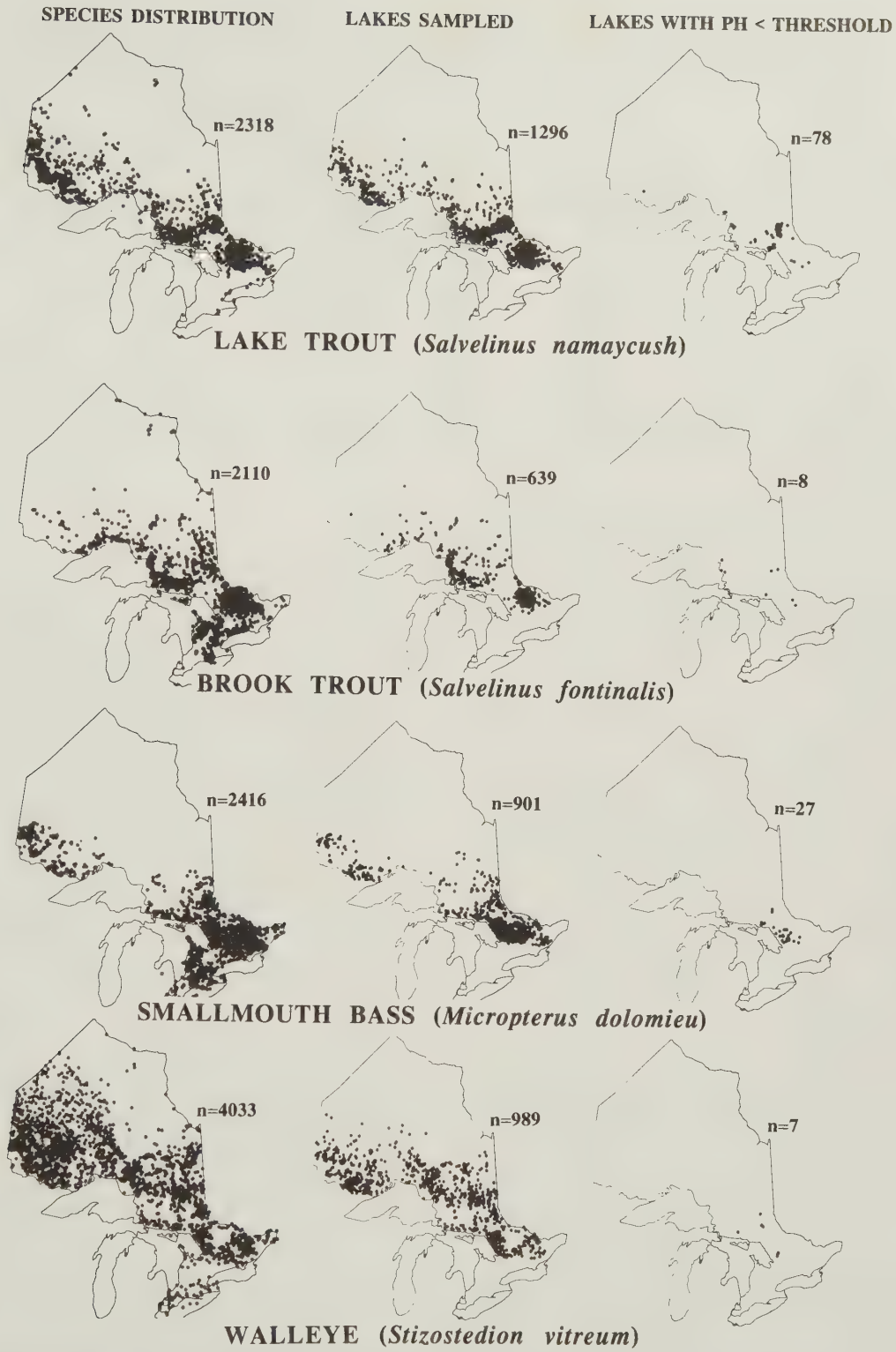

FIG. 2. Distribution of lakes in Ontario known to have contained lake trout, brook trout, smallmouth bass, and walleye. Also shown are the distribution of sampled lakes in the water quality surveys and the location of lakes with pH below the critical level for the species: lake trout, pH < 5.5; brook trout, pH < 5.0; smallmouth bass, pH < 5.5; walleye, pH < 5.5

lakes, and walleye in 4033 lakes in Ontario. Lake watershed code numbers and longitude and latitude were used to assign each lake to a sulphur deposition zone using a SPANS (SPatial ANalysis System) geographical information system.

Lake chemistry data for subjects of the known lake trout, brook trout, smallmouth bass, and walleye lakes were obtained from an extensive survey of lakes conducted by MNR and MOE between 1978 and 1985 (Green et al. 1987; Neary et al. 1990). One water sample was taken from the centre of each lake. Most samples were tube composites (MOE 1979) that were collected in the fall, winter, and summer. Water samples were analyzed for a number of chemical parameters, with pH (100% of sam-

TABLE 1. Sportfish distribution across sulphur deposition zones in Ontario. Zones are defined by lake water quality (Neary et al. 1990) and are illustrated in Fig. 1.

Zone	Total surface area of zone (km^2)	Number of lakes known to have contained sportfish species			
		Lake trout	Brook trout	Smallmouth bass	Walleye
1	465 416	313	17	123	954
2	252 707	572	298	268	1739
3	56 768	95	232	67	584
4[a]	51 050	454	743	216	199
5[a]	85 926	632	666	1495	476
6[a]	53 129	2	47	117	18
7 (Sudbury)[a]	17 022	250	107	130	63
Total	982 018	2318	2110	2416	4033

[a]Zones 4, 5, 6, and 7 classified as "high-deposition" zones with sulphur deposition ≥ 0.75 $g \cdot m^{-2} \cdot yr^{-1}$.

ples), alkalinity (98.9%) and conductivity (93.9%) being the most frequently measured parameters. We used only the pH data for estimation of biological damage (see technical report by Matuszek and Wales (1990) for estimates of "risk" based on alkalinity). All of the pH readings were conducted with electronic pH meters. Distributional information on other chemical parameters is available in Green et al. (1987) and Neary et al. (1990).

A critical pH value for each of the sportfish species was obtained from the literature. Viable populations of a species are not expected to exist at pH levels below the critical value for the species. These estimates were based mainly on netting surveys and field bioassays and are as follows: pH 5.5 for lake trout (Beggs and Gunn 1986), pH 5.0 for brook trout (Beggs and Gunn 1986), pH 5.5 for smallmouth bass (Matuszek 1987), and pH 5.5 for walleye (Wales and Liimatainen 1987). In addition, lakes with pH < 6.0 were classified as lakes with potential damage to sensitivity prey species, following the work of several authors who reported loss of sensitive invertebrate (Keller et al. 1990) and small fish species (Matuszek et al. 1990) at pH values just below 6.0.

Extrapolation of chemical conditions in sampled subsets of lakes to sulphur deposition zone and provincial estimates proceeded from individual watershed unit to tertiary, secondary, and primary watersheds and finally to deposition zone. Extrapolations were conducted when at least one of two criteria were net: >20 lakes were sampled or >75% of the known lakes were sampled. If the conditions for the extrapolation were not met at a particular level, then scaling-up was attempted at the next highest watershed level. These extrapolation procedures were used to increase the probability that the scaling-up process was being performed for sets of lakes that were located on similar geological formations and therefore had similar acid-neutralizing capacities (Shilts 1981). Further details of the extrapolation procedures are available in Matuszek and Wales (1990).

A set of 103 lake trout lakes in the Sudbury zone that had previously been surveyed in 1980 and 1987 (Gunn and Keller 1990) was resampled in 1990 to assess recent temporal trends in water quality for Sudbury lakes. Identical methods of sample collection and analysis for pH, alkalinity, and specific conductance were used in all three years. Between-year variation in chemical parameters was analyzed through ANOVA followed by a Sheffe's multiple range test. Regression analysis was used to assess the relationship between observed chemical changes and particular lake characteristics (distance from Sudbury, lake surface area).

Results

Resource Losses

Lakes sampled during the surveys of 1978–85 (median year 1983) were distributed across all sulphur loading zones in Ontario (Fig. 2), with the exception of zone 1 in the northwest section of the province. However, zone 1 contained very few sportfish lakes and, because of the high buffering capacity of the bedrock and surficial sediments of the area, was not particularly sensitive to acidification (Shilts 1981). In total, pH measurements were collected for 55.9% (n = 1296) of known lake trout lakes, 30.3% (n = 639) of known brook trout lakes, 37.3% (n = 901) of known smallmouth bass lakes, and 24.5% (n = 989) of known walleye lakes in Ontario. The Sudbury zone was well represented in the sampling program. Sample coverage in the Sudbury area was 78.0% (n = 195) of lake trout lakes, 23.4% (n = 25) of brook trout lakes, 36.2% (n = 47) of smallmouth bass lakes, and 47.6% (n = 30) of walleye lakes.

With the exception of walleye lakes, which were largely distributed in northwestern Ontario with low loading of sulphur (≤ 0.75 $gm \cdot m^{-2} \cdot yr^{-1}$), most of Ontario's sportfish lakes were in high-loading (≥ 0.75 $gm \cdot m^{-2} \cdot yr^{-1}$) zones (Table 1). These high-deposition zones accounted for 57.7% of lake trout lakes, 74.4% of brook trout lakes, and 81.4% of smallmouth bass lakes. The Sudbury zone (No. 7) had the smallest surface area (17 022 km^2, 1.7% of Ontario) but contained a substantial number of sportfish lakes (Table 1). The number of lake trout, brook trout, smallmouth bass, and walleye lakes in the Sudbury zone were 250, 107, 130, and 63, respectively, representing 10.8, 5.1, 5.4, and 1.6% of the lakes in Ontario that historically contained these sportfish species (Table 1).

Lake trout was the species most severely affected by acidification, both in terms of absolute numbers and percentage of damaged lakes within loading zones (Table 2). Seventy-eight of the 1296 sampled lake trout lakes in Ontario had a pH below the critical threshold of 5.5 (i.e. stocks either extinct or suffering reproductive failure). By extrapolation, we estimated that acidification has resulted in the loss of 119 lake trout lakes across Ontario (5.1% of total known resource). Most (79.0%) of these losses occurred in the Sudbury zone, where 62 of the sampled lake trout lakes had measured pH <5.5 (Table 2). In total, we estimated that 94 lake trout stocks were lost in the

TABLE 2. Estimated number of low-pH lakes for each sportfish species, by deposition zone and for the entire province of Ontario. Lakes with pH below the critical threshold for the species are expected to have nonreproducing or extinct populations. Lakes with pH < 6.0 are considered to have at least some damage to sensitive prey species.

Species	Deposition zone	Number of lakes				
		Sampled for pH	Sampled with pH < critical	Sampled with pH < 6.0	Estimated with pH < critical	Estimated with pH < 6.0
Lake trout	1	69	0	0	0	0
	2	213	1	1	5	5
	3	63	2	2	4	4
	4	279	8	40	12	67
	5	476	5	46	4	64
	6	1	0	0	0	0
	7 (Sudbury)	195	62	99	94	136
	Ontario total	1296	78	188	119	276
Brook trout	1	3	0	0	0	0
	2	71	0	1	0	1
	3	58	1	5	4	18
	4	156	2	24	14	152
	5	326	2	82	2	140
	6	0	0	0	0[a]	0[a]
	7 (Sudbury)	25	3	10	14	44
	Ontario total	639	8	122	34	355
Smallmouth bass	1	31	0	0	0	0
	2	90	0	0	0	0
	3	32	0	1	0	3
	4	58	0	1	0	4
	5	643	21	96	34	164
	6	0	0	0	0[a]	0[a]
	7 (Sudbury)	47	6	12	18	33
	Ontario total	901	27	110	52	204
Walleye	1	71	0	0	0	0
	2	455	0	2	0	6
	3	186	0	1	0	0
	4	60	1	1	3	3
	5	187	3	20	4	41
	6	0	0	0	0[a]	0[a]
	7 (Sudbury)	30	3	9	7	22
	Ontario total	989	7	32	14	72

[a]Although no lakes were sampled, the zone is located on sedimentary rock (Shilts 1981) and acidification of lakes is unlikely.

Sudbury zone due to acidificiation.

The estimated number of Ontario lakes with pH below the critical level for survival of the three other sportfish species was considerably less than that of lake trout (Table 2). We estimated that 1.6% (n = 34) of brook trout lakes had pH <5.0, 2.2% (n = 52) of smallmouth bass lakes had pH <5.5, and 0.3% (n = 14) of walleye lakes had pH <5.5. The Sudbury zone again contained a large percentage of the lakes in Ontario with critically low pH: 41.2% (n = 14) of the brook trout lakes, 34.6% (n = 18) of the smallmouth bass lakes, and 50.0% (n = 8) of the walleye lakes.

When we used a more conservative pH threshold to define potential damage to sportfish lakes, that is, a pH below which sensitive invertebrates and nonsportfish fish species are lost (pH < 6.0), the provincial estimates were increased, but the substantial influence of the Sudbury zone was still evident (Table 2). The estimated number of lake trout, brook trout, smallmouth bass, and walleye lakes in Ontario with pH < 6.0 was 276 (11.9%), 355 (16.8%), 204 (8.4%), and 72 (1.8%), respectively. The Sudbury zone represented a smaller proportion of the biologically damaged resources, containing 49.2% of the lake trout, 12.3% of the brook trout, 16.2% of the smallmouth bass, and 30.6% of the walleye lakes in Ontario with pH < 6.0 (Table 2). Estimated biological impacts in most loading zones were greatly increased when this more sensitive measure of biological damage (pH < 6.0) was used (Table 2). Zone 5, the area of south-central Ontario that includes much of Algonquin Park and the Haliburton–Muskoka lakes, shows particularly high levels of potential damage to prey species (Table 2).

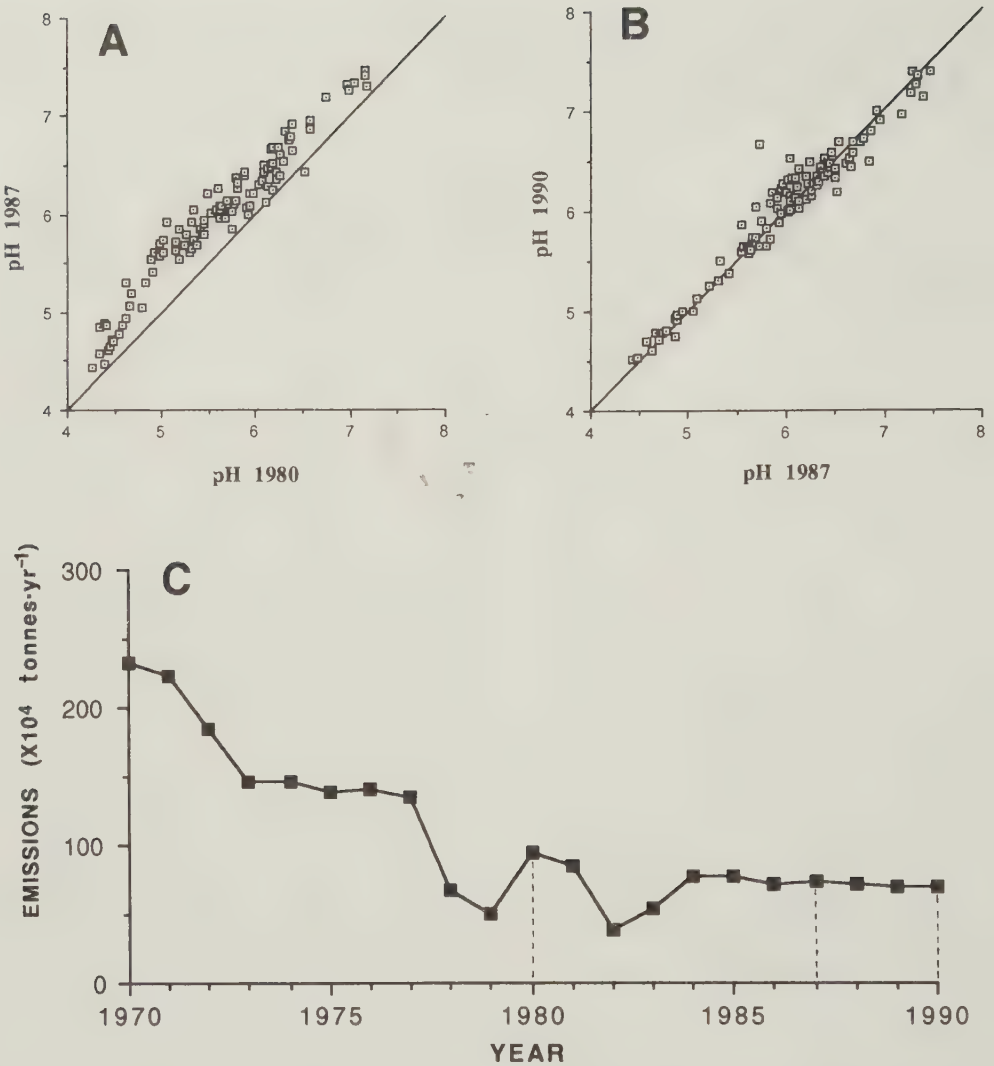

FIG. 3. (A) Comparison of 1980 and 1987 lake water pH in 103 lake trout lakes in the Sudbury area. (B) Lakes were resurveyed in 1990 and results compared with 1987. (C) Emissions of SO_2 from Sudbury smelters during the period 1970–90.

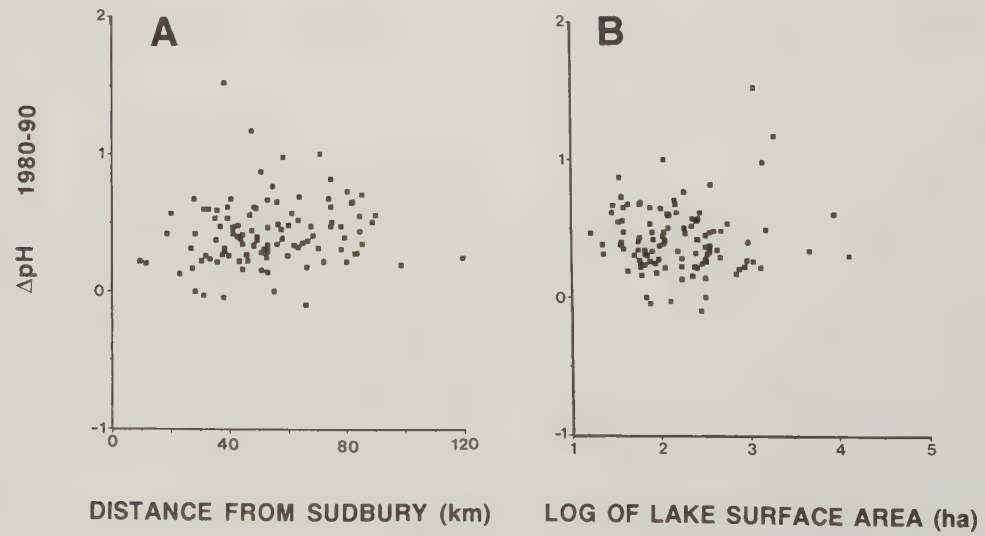

FIG. 4. Observed change in pH between 1980 and 1990 for 103 lake trout lakes in the Sudbury area in comparison with (A) distance from smelters and (B) lake surface area.

Temporal Trends in Water Quality of Sudbury Lake Trout Lakes

Reductions in emissions from Sudbury smelters were accompanied by substantial improvements in water quality of lake trout lakes in the Sudbury zone (Fig. 3). Significant increases in lake water pH occurred between 1980 (pH 5.55 ± 0.14 (mean ± 95% CI)) and 1987 (5.93 ± 0.14), at the end of a long period of emission reductions. No significant increase in lake water pH was detected between 1987 and 1990 (5.98 ± 0.13), a period when emissons had levelled off at approximately 750 000 tonnes $SO_2 \cdot yr^{-1}$ (Fig. 3). The number of critically acidic (pH < 5.5) lake trout lakes declined from 45 in 1980 to 20 in 1987 and remained at 20 in 1990.

Alkalinity exhibited the same increasing trend as did pH, with sample means of 1.89 (±0.91) $mg \cdot L^{-1}$ in 1980, 3.08 (±0.99) $mg \cdot L^{-1}$ in 1987, and 3.21 (±1.02) $mg \cdot L^{-1}$ in 1990. Specific conductance declined as the lakes became less acidic (1980, 49.4 ± 4.9 $\mu S \cdot cm^{-1}$; 1987, 43.5 ± 5.8 $\mu S \cdot cm^{-1}$; 1990, 43.5 ± 6.4 $\mu S \cdot cm^{-1}$). Again, statistically significant changes ($p < 0.05$) were observed only between 1980 and 1987.

The chemical recovery observed during 1980–87 affected virtually all lake trout lakes in the Sudbury zone. There were no significant ($p < 0.05$) relationships between the observed pH change and lake size or distance from the smelters (Fig. 4).

Discussion

Atmospheric emissions from the Sudbury smelters were responsible for most of the acidification-related sportfish losses in Ontario. In the early 1980s, at the time of the initial surveys, the Sudbury area contained from 34.6 to 79.0% of the sportfish lakes with pH below the critical thresholds.

Lake trout lakes were particularly vulnerable to acidification damage. This species is almost exclusively confined to recently glaciated lakes on Precambrian Shield bedrock, lakes that are typically slightly acidic with lower alkalinity and total dissolved solids than non-lake-trout lakes (Martin and Olver 1976; Johnson et al. 1977). The high vulnerability of lake trout waters to acidification was evident within our defined acid deposition zones. For example, in the Sudbury zone, an estimated 37.6% of lake trout lakes had pH below pH 5.5. For walleye and smallmouth bass, species with the same critical threshold as lake trout (i.e. pH < 5.5), the percentages of lakes with critically acidic water were only 11.1 and 13.8%, respectively.

Rapid chemical recovery of Sudbury area lakes has occurred following emission reductions at Sudbury smelters. Some biological recovery of these damaged lakes has also been observed (Keller et al. 1992a). Gunn and Keller (1990) reported that a remnant population of lake trout began to successfully reproduce in Whitepine Lake when pH rose from 5.4 in 1980 to 5.9 in 1988. The number of taxa of benthic invertebrates in the lake rose from 39 to 72 during the recovery period. Keller and Yan (1991) observed increases in species richness of zooplankton in a number of Sudbury lakes where water quality improvements had occurred. Several of the "new" species in these lakes were acid-sensitive species such as *Epischura lacustris*.

In spite of the encouraging signs of recovery in the Sudbury area, a large number of lakes remain acidic with elevated levels of metals. The water quality improvements in acidified lake trout waters, observed between 1980 and 1987 (Gunn and Keller 1990), ceased after emissions levelled off. We observed no change between the 1987 and 1990 surveys. Keller et al. (1992b), in an accompanying paper, document a similar pattern for Sudbury lakes, with no change or even some declines in lake pH in the mid- to late 1980s. These findings provide strong support for additional controls on industrial sources of air-pollutants to allow affected lakes to continue to recover.

Our estimates of acidification-related damage to sportfish populations in Ontario are relatively low compared with other measures of damage to biota in Ontario. Neary et al. (1990) estimated that 19 000 lakes had pH < 6.0 and were expected to have suffered some damage among sensitive organisms. Less than half (7300) of these "damaged" lakes were in the Sudbury zone. Use of the pH 6.0 threshold greatly increased the extent of damage in our sportfish set of lakes, but it is difficult to assign these losses to particular species or to predict food web effects (Schindler 1988). We also cannot assess the extent of genetic loss that has accompanied acidification. Much remains to be learned about natural recovery rates and processes and whether rehabilitation measures such as lake neutralization and reintroductions with hatchery-reared fish (or prey species) can effectively return lakes to their indigenous state.

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References

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Beamish, R. J., W. L. Lockhart, J. C. Van Loon, and H. H. Harvey. 1975. Long term acidification of a lake and resulting effects on fishes. Ambio 4: 98–102.

Beggs, G. L., and J. M. Gunn. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711–717.

Dillon, P. J., R. A. Reid, and R. Girard. 1986. Changes in the chemistry of lakes following reductions of SO_2 emissions. Water Air Soil Pollut. 31: 59–66.

Dodge, D. G., G. A. Goodchild, I. MacRichie, J. C. Tilt, and D. G. Waldriff. 1985. Manual of instructions: aquatic habitat inventory surveys. Ontario Ministry of Natural Resources, Toronto, Ont. 169 p.

Green, D., J. Matuszek, and D. Wales. 1987. Extensive survey data report. Ont. Fish. Acid. Rep. Ser. No. 87–12: 89 p.

Gunn, J. M., and W. Keller. 1990. Biological recovery of an acid lake following reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

Harvey, H. H. 1975. Fish populations in a large group of acid-stressed lakes. Verh. Int. Ver. Limnol. 19: 2406–2417.

Harvey, H. H., and C. Lee. 1982. Historical fisheries changes related to surface water pH changes in Canada, p. 45–55. *In* R. E. Johnson [ed.] Acid rain/fisheries. American Fisheries Society, Bethesda, MD.

Johnson, M. G., J. H. Leach, C. K. Minns, and C. H. Olver. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui*). J. Fish. Res. Board Can. 34: 1592–1601.

Jones, M. L., C. K. Minns, D. R. Marmorek, and F. C. Elder. 1990. Assessing the potential damage to inland lakes in eastern Canada due to acidic deposition: II. Application of the regional model. Can. J. Fish. Aquat. Sci. 47: 67–80.

Keller, W. 1978. Limnological observations on the aurora trout lakes. Ont. Minst. Environ. Tech. Rep. 49 p.

Keller, W., J. M. Gunn, and N. D. Yan. 1992a. Evidence of biological recovery in acid stressed lakes near Sudbury, Canada. Environ. Pollut. 78: 79–85.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

KELLER, W., J. R. PITBLADO, AND J. CARBONE. 1992b. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 25–32.

KELLER, W., AND N. D. YAN. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

KELLER, W., N. D. YAN, K. E. HOLTZE, AND J. R. PITBLADO. 1990. Inferred effects of lake acidification on *Daphnia galeata mendota*. Environ. Sci. Technol. 24: 1259–1261.

KELSO, J. R., AND J. M. GUNN. 1984. Responses of fish communities to acid waters in Ontario, p. 105–115. *In* G. R. Hendrey [ed.] Early biotic responses to advancing lake acidification. Butterworth Publishers, Stoneham, MD.

KELSO, J. R. M., M. A. SHAW, C. K. MINNS, AND K. H. MILLS. 1990. An evaluation of the effects of atmospheric acidic depositin on fish and the fisheries resource of Canada. Can. J. Fish. Aquat. Sci. 47: 644–655.

MARTIN, N. V., AND C. H. OLVER. 1976. The distribution and characteristics of Ontario lake trout lakes. Ont. Minst. Nat. Resour. fish. Wildl. Res. Rep. 97: 30 p.

MATUSZEK, J. E. 1987. An assessment of the current impact and potential risks of acid deposition on smallmouth bass populations in Ontario. Ont. Fish. Acid. Rep. Ser. No. 87-09.

MATUSZEK, J. E., AND G. L. BEGGS. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

MATUSZEK, J. E., J. GOODIER, AND D. L. WALES. 1990. The occurrence of Cyprinidae and other small fish species in relation to pH in Ontario lakes. Trans. Am. Fish. Soc. 119: 850–861.

MATUSZEK, J. E., AND D. L. WALES. 1990. The status of lake trout, brook trout, smallmouth bass, and walleye populations in Ontario with respect to acidification. Ont. Fish. Acid. Rep. Ser. No. 90–16.

MINNS, C. K. 1989. Factors affecting fish species richness observed in Ontario's inland lakes. Trans. Am. Fish. Soc. 118: 533–545.

MINNS, C. K., J. E. MOORE, D. W. SCHINDLER, AND M. L. JONES. 1990. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. III. Predicted impacts on species richness in seven groups of aquatic biota. Can. J. Fish. Aquat. Sci. 47: 821–830.

MOE (ONTARIO MINISTRY OF THE ENVIRONMENT). 1979. Determination of susceptibility to acidification of poorly buffered surface waters. Ont. Minist. Environ. Report, Toronto, Ont. 21 p.

NEARY, B. P., AND P. J. DILLON. 1988. Effects of sulphur deposition on lake water chemistry in Ontario, Canada. Nature (Lond.) 333: 340–343.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ont. Minist. Environ. Rep., Tornto, Ont. 170 p.

OCTF (ONTARIO/CANADA TASK FORCE). 1982. Report of the Ontario/Canada Task Force for the development and evaluation of air pollution abatement options for INCO Limited and Falconbridge Nickel Mines Limited in the Regional Municipality of Sudbury, Ontario. Intergovernmental Task Force Report, Toronto, Ont. 225 p.

OWRC (ONTARIO WATER RESOURCES COMMISSION). 1970. Preliminary report on the influence of industrial activity on the lakes in the Sudbury area (1969–1970). Ontario Water Resources Commission, Toronto, Ont. 34 p.

SCHINDLER, D. W. 1988. Effects of acid rain on freshwater ecosystems. Science (Wash., DC) 239: 149–157.

SCHINDLER, D. W., S. E. KASIAN, AND R. H. HESSLEIN. 1989. Biological impoverishment in lakes of the midwestern and northeastern United States. Environ. Sci. Technol. 23: 573–580.

SHILTS, W. W. 1981. Sensitivity of bedrock to acid precipitation: modification by glacial processes. Geol. Surv. Can. Pap. 81-14: 7 p.

WALES, D. L., AND G. L. BEGGS. 1986. Fish species distributions in relation to lake acidity in Ontario. Water Air Soil Pollut. 30: 601–609.

WALES, D. L., AND V. A. LIIMATAINEN. 1987. Preliminary assessment of the current impact and potential risk of acidic deposition on walleye populations in Ontario. Ont. Fish. Acid. Rep. Ser. No. 87-11: 29 p.

WATT, W. D., C. D. SCOTT, AND W. J. WHITE. 1983. Evidence of acidification of some Nova Scotian rivers and its impact on Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 40: 462–473.

Prediction of Lake Trout (*Salvelinus namaycush*) Presence in Low-Alkalinity Lakes near Sudbury, Ontario

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Surveys of 30 low-alkalinity lake trout (*Salvelinus namaycush*) lakes near Sudbury, Ontario, were conducted to assess factors that affect lake trout presence under acidification stress. At the time of the surveys the lakes varied widely in pH (4.5–6.9), concentrations of toxic metals (Al 12–300 $\mu g \cdot L^{-1}$), and the status of lake trout populations (extinct–abundant). Fish community structure (species richness, species assemblages) reflected and was readily predicted from measured water quality variables. A PCA factor composed of pH, alkalinity, and conductivity was the variable that best predicted lake trout presence (correct discrimination (>92%). The results of this study provide managers with easily obtainable predictors for monitoring lake trout status under changing levels of acidic deposition.

Des études sur 30 lacs à touladi (*Salvelinus namaycush*) de faible alcalinité près de Sudbury (Ontario) ont été menées pour évaluer les facteurs qui influent sur la présence de cette espèce dans des conditions de stress acide. Au moment de l'étude, les caractéristiques des lacs variaient considérablement sur le plan du pH (4,5 à 6,9), des concentrations de métaux toxiques (Al 12 à 300 $\mu g \cdot L^{-1}$) et de la situation des populations de touladi (disparition à abondance). La structure de l'ichtyofaune (richesse en espèces, associations d'espèces) correspondait aux variables de la qualité de l'eau mesurées et pouvait être prédite sur cette base. Le facteur PCA composé du pH, de l'alcalinité et de la conductivité s'est révélé être la variable qui permettait de prédire avec le plus de justesse la présence du touladi (discrimination correcte >92 %). Les résultats de cette étude fournissent aux gestionnaires des paramètres de prévision faciles à obtenir pour la surveillance de la situation du touladi dans des conditions variables de dépôts acides.

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Lake trout (*Salvelinus namaycush*) lakes in Ontario are a highly valued fisheries resource. Less than 1% of Ontario lakes contain this species. However, these lakes (n = 2318) support approximately 20–25% of the worlds distribution of the species (Martin and Olver 1976; Olver et al. 1990). Therefore, fisheries managers in Ontario have a special responsibility to protect lake trout lakes from environmental stresses.

Lake acidification is an environmental problem to which lake trout populations are particularly vulnerable (Beggs et al. 1985). Lake trout usually occur in poorly buffered, oligotrophic lakes (Martin and Olver 1976; Beggs et al. 1985), and the species is highly sensitive to low-pH waters (Johnson et al. 1987; Mills et al. 1987; Hutchinson et al. 1989). Natural populations are also frequently sparse in these low-nutrient lakes, making it difficult for managers to directly sample populations without potentially damaging them.

Simple and perhaps more indirect measures of lake trout population status are needed to assess the effects of changes in acid deposition over large geographic areas. Measures of lake morphometry or water chemistry are frequently correlated with the presence, abundance, and production of fish species (Johnson et al. 1977; Tonn and Magnuson 1982; Rahel 1986; Marshall and Ryan 1987). These parameters may be useful for regional assessments of lake trout populations. Similarly, measures of size distribution, abundance, and composition of prey or predator species are also potentially useful indices of the status of fish populations (Mills and Schiavone 1982; Evans et al. 1987; Kitchell and Carpenter 1987; McQueen et al. 1989).

The objective of our study was to develop and test predictive relationships of lake trout presence using readily available data from field surveys. These empirical relationships were derived from chemical, physical, and biological surveys of lake trout lakes near Sudbury, Ontario, an area severely affected by acid deposition (Beamish and Harvey 1972; Matuszek et al. 1992).

Methods

Lake Selection and Field Survey Techniques

Thirty lake trout lakes from the Sudbury Acid Deposition Zone were used for this study (Fig. 1). The Sudbury zone is a

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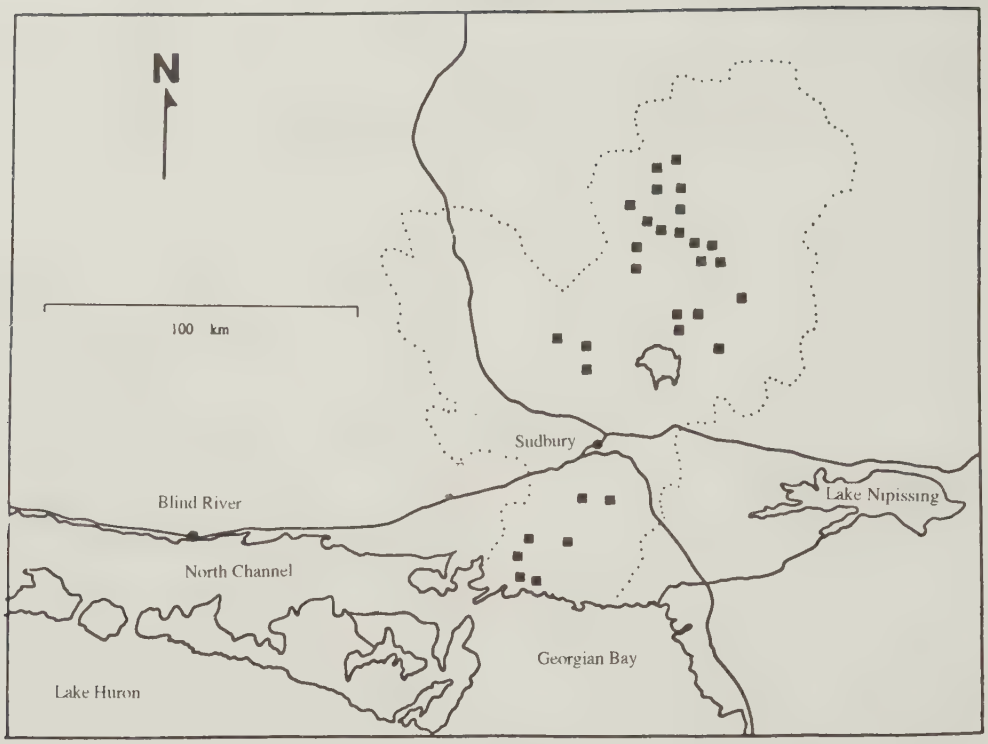

FIG. 1. Location (■) of the 30 lake trout lakes used in the study. All lakes are within the boundary of the Sudbury Deposition Zone (dotted line) as defined by Neary et al. (1990).

17 000 km^2 area where SO_4 deposition originates mainly from local industries (Neary et al. 1990).

Lakes were selected that historically supported naturally reproducing lake trout populations (J. Gunn, unpubl. data) but currently varied widely in pH (pH 4.5–6.9) and alkalinity (−1.8–3.3 mg·L^{-1} as $CaCO_3$) (Table 1). These lakes were relatively small (17–1007 ha), dilute (conductivity 22–43 μS·cm^{-1}), and clear (dissolved organic carbon (DOC) 0.2–4.6 mg·L^{-1}). All lakes were located in forested areas underlain with granitic bedrock of the Precambrian Shield. Distances to the Copper Cliff smelters ranged from 22 to 100 km. Only three of the lakes (Nelson, Wavy, and White Oak) were within the area (<30 km from smelters) receiving high deposition of metal particulates (Keller and Pitblado 1986; Keller et al. 1992).

There is little historical information on the water quality of these study lakes. However, paleolimnological reconstructions of past conditions indicated that some Sudbury lakes began to acidify more than 40 yr ago (Dixit et al. 1989). Most of the lakes in the Sudbury area that are currently acidic had circumneutral pH during the preindustrial period (Dixit et al. 1992).

Assessment netting occurred during May to the first week of September in 1988 and 1989. Netting effort consisted of up to six overnight sets of experimental gill nets (five 15.2-m panels of 2.5-, 3.8-, 5.1-, 6.3-, and 7.6-cm stretched monofilament mesh), small-mesh trap nets (0.9-cm mesh; 1.22-m box; Beamish 1972), and Plexiglas minnow traps (Casselman and Harvey 1973). Up to 60 overnight sets of baited wire-mesh minnow traps were also employed on each lake. Gill nets were set to sample the epilimnion and the well-oxygenated (>4 ppm O_2) strata of the hypolimnion. Trap nets and minnow traps sampled the shallow (<4 m) littoral zone. Sampling mortality for lake trout was limited by removing gill nets as soon as the lake trout catch exceeded 24 fish. This "limited kill" procedure reduced gillnet sampling effort to a minimum of two sets in some lakes (mean number of sets = 4.7 per lake).

The total number and fresh weight biomass of each species were recorded for each gear type. Species identifications, with the exception of species of Cyprinidae, were conducted in the field. Subsamples of cyprinids were collected for later identification following Scott and Crossman (1973).

Temperature and oxygen profiles, lake surface area (A_0), maximum (Z_{max}) and mean depth ($\bar{Z}$), lake volume, and Secchi disc transparency were measured at the time of the fish surveys according to methods described in Dodge et al. (1985). Epilimnetic tube composite water samples were taken at midlake during stratification in September 1989. Collection and analysis of water samples followed OMOE (1981). All reported metal levels are total concentrations.

Statistical Analyses

Relationships between the fish species present and measured physicochemical variables were assessed using principal components analysis (PCA) (Green 1979). Because of incomplete species identifications, all minnow species were combined as "cyprinids." Similarly, because few centrarchids were collected, all centrarchid species (smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), pumpkinseed (*Lepomis gibbosus*), bluegill (*L. macrochirus*), and rock bass (*Ambloplites rupestris*)) were pooled as "centrarchids." Only fish taxa that occurred in at least 10% of the lakes were used in the analyses. Factor scores were calculated for the three most significant factors (those with eigenvalues >1). Subsequently, we determined the correlation between these factor scores for each lake and 14 physicochemical variables.

Discriminant analyses (SPSS 1986) were used to assess factors related to lake trout presence. The data set was split to

TABLE 1. Selected morphometric and chemical characteristics of 30 lake trout lakes near Sudbury, Ontario. Water chemistry samples were collected during September 1989. Presence of lake trout and other fish species from the 1988 and 1989 lake surveys is indicated.

Lake[a]	Lat.	Long.	Elev. (m)	A_0 (ha)	Z_{max} (m)	pH	TIP alk. ($mg \cdot L^{-1}$)	Cond. ($\mu S \cdot cm^{-1}$)	Ca ($mg \cdot L^{-1}$)	Al ($\mu g \cdot L^{-1}$)	Cu ($\mu g \cdot L^{-1}$)	Ni ($\mu g \cdot L^{-1}$)	Lake trout (+/−)	No. of fish species[b]
Aylmer No. 37[2]	46°53′	80°43′	312	37	19	4.6	−1.8	39	1.9	280	3	18	−	0
Bell[2]	46°08′	81°12′	226	281	27	5.8	0.2	37	2.9	70	4	11	+	12
Bigwood[1]	46°51′	81°05′	373	266	58	5.9	0.7	32	2.9	65	2	5	+	7
Bluesucker[2]	47°10′	80°36′	343	145	21	5.4	−0.2	30	2.2	110	0	4	+	11
Bowland[2]	47°05′	80°50′	390	108	28	6.0	0.9	32	3.1	32	1	2	+	2
Dewdney[1]	46°52′	80°40′	296	176	34	4.8	−1.1	38	2.5	210	3	21	−	1
Florence[1]	47°15′	80°33′	366	1007	38	4.8	−0.7	37	2.4	270	1	6	−	4
George[1]	46°02′	81°24′	189	182	40	6.2	0.2	30	2.3	35	1	5	+	9
Great Mountain[1]	46°09′	81°22′	227	192	38	5.2	−0.8	30	2.0	86	2	10	−	2
Iron[2]	46°57′	80°21′	343	72	27	5.8	0.1	36	3.4	24	1	5	+	12[c]
Jerry[1]	47°22′	80°39′	419	56	35	5.1	−0.6	30	2.1	180	0	3	−	1
Kelly No. 27[1]	46°47′	80°32′	297	17	17	5.8	−0.3	34	3.1	53	1	14	−	1
Laundrie[1]	47°07′	80°52′	396	375	20	5.8	0.9	29	2.7	41	1	0	+	4
Linger[2]	47°05′	80°30′	312	70	20	5.7	0.0	31	2.7	61	1	3	+	6
Lulu[2]	47°24′	80°45′	450	81	23	5.5	−0.2	26	2.0	92	0	0	+	6
Lumsden[1]	46°41°	81°07′	241	22	24	5.1	−0.6	28	1.4	140	2	7	−	0
Marina[1]	47°24′	80°40′	389	37	17	5.4	0.1	30	2.4	160	10	26	+	4
Marjorie[2]	46°55′	80°37′	325	75	35	4.5	−2.0	42	1.5	300[d]	3	19	−	0
Michaud[2]	46°49′	81°14′	404	148	24	5.7	0.1	28	2.3	74	1	4	+	5
Nelson[2]	48°44′	81°05′	348	309	51	6.6	1.0	35	3.3	20[e]	2	5	+	8
Pilgrim[2]	47°11′	80°41′	358	123	25	5.6	−0.1	26	2.1	46	1	3	+	6
Regan[1]	47°14′	80°47′	396	122	38	6.9	3.3	36	3.5	12	0	0	+	11[c]
Seagram[2]	47°06′	80°32′	314	102	20	5.4	0.3	22	2.8	96	1	4	+	8
Solace[1]	47°11′	80°42′	366	317	57	5.7	0.0	31	2.6	61	1	3	+	7
Threenarrows[2]	46°05′	81°28′	197	948	52	6.0	0.1	31	2.3	47	2	6	+	9
Wavy[1]	46°18′	81°06′	262	255	34	4.8	−1.5	43	2.3	200	18	77	−	1
White Oak[2]	46°18′	81°00′	236	273	43	5.3	−0.5	40	2.7	110	12	69	−	2
Whitepine[2]	47°17′	80°50′	412	67	22	5.8	0.3	28	2.2	41	0	0	+	7[c]
Yorston[2]	47°03′	80°32′	327	351	45	6.2	0.9	38	4.3	18	2	3	+	7
Yorston R. Pool[1]	47°07′	80°34′	328	35	20	5.5	−0.1	30	2.5	61	1	5	+	8[c]

[a]1, lakes randomly selected for derivation of discriminant functions; 2, lakes used to test discriminant functions.
[b]Number of all species captured in a variety of geartypes.
[c]Incomplete cyprinid species identification.
[d]Estimated value.
[e]OMOE unpublished data.

develop and test these discriminant functions. Random numbers were used to select 14 lakes for the function derivation set, such that seven lakes had lake trout present and seven lakes had lake trout currently absent. The accuracy of the a posteriori classification of lake trout presence/absence (from the netting surveys) was used as a measure of the classification power of the derived discriminant function. The functions with the highest correct classifications were then applied to the remaining 16 lakes (Table 1) to test the predictive power of the derived functions.

Results

Composition of Fish Communities

A total of 34 species of fish were captured in the study lakes (Table 1). Lake trout was the most common species, occurring in 20 of the 30 lakes (67%). Other common species included white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*), and Iowa darter (*Etheostoma exile*), with frequencies of occurrence of 60, 57, and 30%, respectively. Three lakes were fishless (Table 1). The fishless lakes were very acidic (pH 4.5–5.1) with high levels of Al (140–300 $\mu g \cdot L^{-1}$).

The number of species per lake, or species richness, varied from 0 to 12. Species richness increased with lake area ($\log_{10}$ (no. of species) = $-0.27 + 0.43 \cdot (\log_{10}$ (area)), $p < 0.05$) (Fig. 2A), which is typically the case (Tonn and Magnuson 1982; Matuszek and Beggs 1988; Matuszek et al. 1990). However, the regression relationship between species richness and lake area in these low-alkalinity lakes account for little of the observed variation ($R^2 = 0.30$). When the observed number of species in our set of lakes was compared with the "expected number" of species in similar sized, but well-buffered lakes ($\log_{10}$ (no. of species) = $0.52 + 0.22 \cdot (\log_{10}$ (area)); Matuszek et al. 1990), it appeared that some of the low-pH lakes had lost more than 10 fish species prior to our survey (Fig. 2B).

To examine relationships between current species composition and physical and chemical lake characteristics, the fish species present were classified into three groups, or assemblages, through PCA. The PCA classification explained 66.0% of the variation in the species presence data (Table 2). The first assemblage (PCA factor 1) consisted of species classified as acid sensitive in various previous studies (e.g. Holtze and Hutchinson 1989; Matuszek et al. 1990). Lake trout, white sucker, cyprinids, and Iowa darter had significant ($p < 0.01$) component loadings in this group. Correlation of

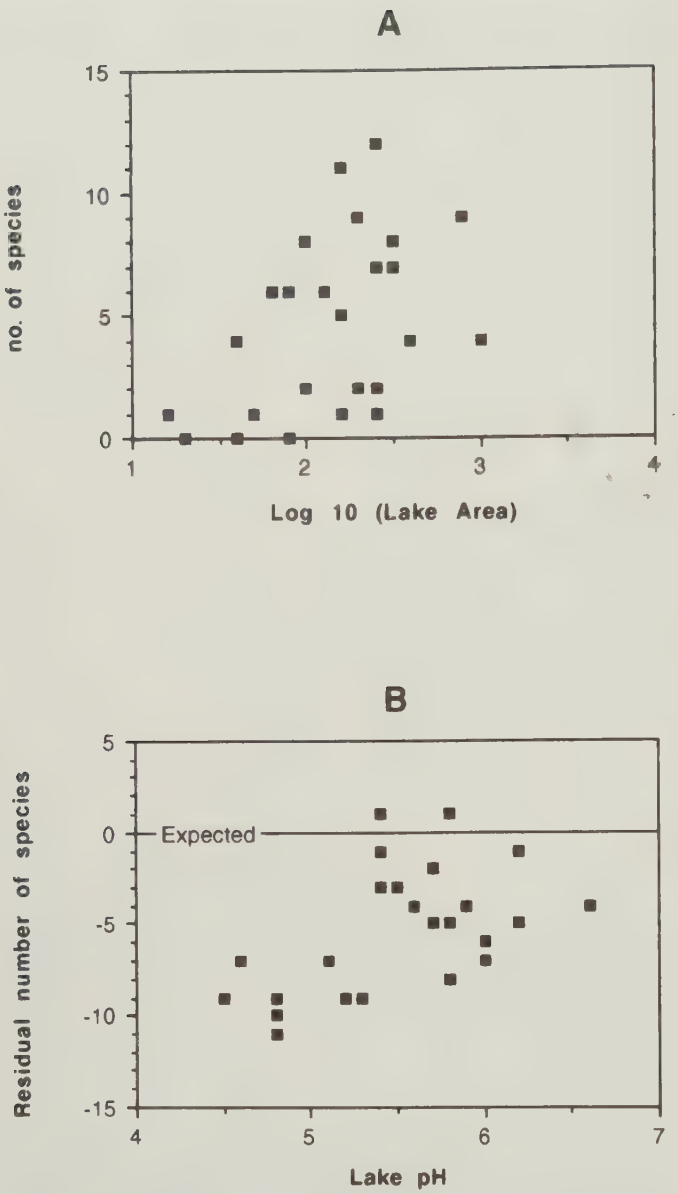

FIG. 2. Relationship between (A) number of fish species and lake area and (B) residual number of species (expected minus observed number of species) and lake water pH. Points lying below the 0 line in Fig. 2B indicate lakes having fewer species than predicted from lake area using the relationship $\log_{10}$ (no. of species) = 0.52 + 0.22·($\log_{10}$ (area)) from Matuszek et al. (1990). Only lakes with complete cyprinid species identification (n = 26) were used.

the factor scores from the PCA with physicochemical variables confirmed that the presence of assemblage 1 taxa was positively related to pH and alkalinity and negatively related to metals leached from the terrestrial watershed, such as Al, and to metals atmospherically transported to the lakes, such as Ni (Table 3).

The second assemblage contained relatively acid-tolerant species (brook trout (*Salvelinus fontinalis*), brown bullhead (*Ameiurus nebulosus*), yellow perch, and northern pike (*Esox lucius*)) and appeared to be related to base cation (Ca, Mg) concentrations (Table 3). Brook trout and brown bullhead are associated with each other (+ sign in factor 2) but not with yellow perch and northern pike (− sign in factor 2). That is, all four species are acid tolerant, but they are not all associated equally with one another. For example, it is well known that

TABLE 2. Fish species assemblages suggested by the first three factors of the varimax rotated factor matrix of fish presence/absence. Statistically significant correlations are indicated (*$p < 0.05$, **$p < 0.01$).

Variable	Factor 1	Factor 2	Factor 3
Lake trout	0.83**	−0.12	0.25
Brook trout	0.32	0.59**	−0.13
Brown bullhead	0.34	0.72**	0.09
Centrarchid	0.15	−0.15	0.92**
Cisco	−0.08	−0.05	0.81**
Cyprinid	0.72**	0.25	−0.11
Iowa darter	0.67**	0.21	−0.30
Northern pike	0.45*	−0.52**	0.24
White sucker	0.85**	0.01	0.14
Yellow perch	0.15	−0.81**	0.14
Eigenvalue	2.95	2.40	1.24
% variance	29.5	24.0	12.4
Cumulative % variance explained	29.5	53.5	66.0

TABLE 3. Pearson correlation coefficients for correlations between fish assemblage factor scores and observed physicochemical variables. Statistically significant correlations are indicated (*$p < 0.05$, **$p < 0.01$).

Variable	Factor 1	Factor 2	Factor 3
pH	0.60**	−0.33	0.30
Alkalinity	0.64**	−0.29	0.10
Conductivity	−0.31	−0.19	−0.07
Ca	0.49**	−0.25	0.14
Mg	0.45*	−0.39*	0.25
Al	−0.62**	−0.12	−0.29
Cu	−0.26	−0.20	−0.15
Ni	−0.52**	−0.09	−0.15
Fe	−0.09	0.35	−0.16
Elevation	0.35	0.07	−0.69**
Surface area	0.23	−0.20	0.35
Maximum depth	−0.02	−0.24	0.32
Mean depth	−0.21	0.04	0.26
Volume	0.11	−0.18	0.38*
Secchi	0.26	0.08	−0.38*

brook trout are displaced by introduced perch populations (Fraser 1978).

The third assemblage, characterized by the presence of centrarchids and cisco (*Coregonus artedi*), was associated with lakes lower in elevation and larger in volume than other lake trout lakes in the study set (Tables 2, 3).

Lake Trout Presence/Absence

The presence or absence of lake trout at the time of survey was readily predicted from the measured water quality. The lakes with lake trout present had significantly (ANOVA; $p < 0.05$; mean ± SD) higher pH (5.9 ± 0.4) and alkalinity (0.4 ± 0.8 mg·L^{-1}) and lower concentrations of Al (53 ± 35 μg·L^{-1}) and Ni (5 ± 0.01 μg·L^{-1}) than the lakes with lake trout absent (pH 5.0 ± 0.4, alkalinity −1.0 ± 0.6 mg·L^{-1}, Al 180 ± 85 μg·L^{-1}, Ni 24 ± 0.03 μg·L^{-1}). The results for Al and Ni were confirmed a posteriori by the Mann–Whitney nonparametric test because of heterogeneity in the data set. The minimum pH level and maximum concentration of Al at which lake trout were present were pH 5.4 and Al 160 μg·L^{-1} (Table 1).

Alkalinity was the single variable that offered the greatest potential for classifying lake trout presence/absence. The dis-

TABLE 4. Prediction of lake trout presence (LTp) and absence (LTa) in low-alkalinity lakes using various statistically significant discriminant functions. The discriminant functions were derived using data from a randomly selected set of lakes (I) where presence and absence of lake trout was confirmed through the netting survey. The discriminant functions that produced the highest correct classification were then applied to the remaining lakes, the test set (II).

Function variable(s)	Observed LT status	No. of lakes	Status predicted by discriminant analysis		Overall correct classification (%)
			LTp	LTa	
I. Derivation set					
Al	Presence	7	5 (71.4%)	2 (28.6%)	78.6
	Absence	7	1 (14.3%)	6 (85.7%)	
PCA factor 1[a]	Presence	7	5 (71.4%)	2 (28.6%)	76.9
	Absence	6	1 (16.7%)	5 (83.3%)	
Alkalinity	Presence	7	6 (85.7%)	1 (14.3%)	92.9
	Absence	7	0 (0.0%)	7 (100.0%)	
pH	Presence	7	5 (71.4%)	2 (28.6%)	78.6
	Absence	7	1 (14.3%)	6 (85.7%)	
PCA factor 1[b]	Presence	7	6 (85.7%)	1 (14.3%)	92.9
	Absence	7	0 (100.0%)	7 (100.0%)	
II. Test set					
PCA factor 1[b]	Presence	13	12 (92.3%)	1 (7.7%)	93.8
	Absence	3	0 (0.0%)	3 (100.0%)	
Alkalinity	Presence	13	10 (76.9%)	3 (23.1%)	81.3
	Absence	3	0 (0.0%)	3 (100.0%)	

[a]Factor 1 score for PCA of 11 physical and chemical variables. Variables that had significant loadings on factor 1 were Al and pH.

[b]Factor 1 score for PCA of three "standard" variables in assessment of acid-sensitive lakes: pH, alkalinity, and conductance.

criminant analyses using only total inflection point (TIP) alkalinity (canonical correspondence = 0.68, $\chi^2(1) = 7.19$, $p < 0.005$, $n = 14$) correctly classified the lake trout status in 92.9% of the 14 lakes used for function derivation (Table 4). Alkalinity predicted lake trout absence (LTa) with 100.0% accuracy, but lake trout presence (LTp) was predicted with only 85.7% accuracy. Other variables related to acidification, such as pH or Al, did not classify the present status of lake trout as well as alkalinity (correct classification of both pH and Al = 78.6%). A PCA factor of 11 physicochemical variables also proved a poor classifier (overall correct classification = 76.9%).

Extensive data on metal and major ion concentrations in Ontario's lake trout lakes are not available (Green et al. 1987). Therefore, further analyses were conducted using only the variables pH, alkalinity, and conductivity, for which large numbers of lake trout lakes have been sampled (Matuszek and Wales 1990).

When pH, conductivity, and alkalinity were combined in a PCA, and the resulting factor score (PCA factor 1[b]) used as a discriminating variable, the discriminant function (canonical correspondence = 0.64, $\chi^2(1) = 5.43$, $p = 0.02$) was a strong classifier (overall correct classification = 92.9%).

The two discriminant functions that classified lake trout status the highest (alkalinity and PCA factor 1[b]) were computed for our 16-lake test set to determine the predictive ability of the two functions in other lake trout lakes. The PCA factor 1[b] was more accurate at predicting present lake trout status (total correct classification 93.8%) than alkalinity (correct classification 81.3%). Both functions were 100% accurate at predicting lake trout absence, but the factor score 1[b] was more accurate at predicting lake trout presence (92.3%) than was alkalinity (76.9%).

Discussion

The results of our surveys of low-pH lake trout lakes in the Sudbury area are generally consistent with results from previous studies in this (Beamish 1976; Harvey and Lee 1982; Beggs and Gunn 1986) and many other parts of the world. The decline in number of species of biota, the loss of acid-sensitive species, and the increase in concentration of toxic metals such as Al are now a well-known suite of acidification-related effects (reviewed in Baker et al. 1990; RMCC 1990). The Sudbury area provides a rather extreme example of these damaging effects of acid deposition on sportfish resources. In an accompanying paper, Matuszek et al. (1992) estimates that 37.6% of the lake trout populations in the Sudbury area were lost because of lake acidification.

Lake trout is a particularly well-studied species with regard to the effects of lake acidification. Data on lake trout from a wide variety of experimental approaches, including field surveys (Beggs et al. 1985; Kelso et al. 1986; Schofield and Driscoll 1987; Krester et al. 1989), ecosystem manipulations (Mills et al. 1987; Gunn et al. 1990), field bioassays (Johnson et al. 1987), and laboratory bioassays (Hutchinson et al. 1989), are now available to predict how individual lake trout populations will respond to changes in lake acidity. However, predicting changes in the distribution of lake trout resources on a regional basis remains more difficult.

For most species, the lack of survey information makes it impossible to accurately predict species distributions. However, for lake trout, such estimates may be possible. Lake trout distributions appear to be quite predictable from physical and chemical characteristics of the lakes they occupy (Kelso et al. 1986), and extensive inventory information on lake trout lakes

is available in some areas (Beggs et al. 1985; Krester et al. 1989; Carl et al. 1990).

Lake trout lakes are generally larger, clearer, deeper, and at higher elevation than non-lake-trout lakes (Martin and Olver 1976). Physical variables that have proven useful for identifying lake trout lakes through discriminant or gradient analyses included water depth (Johnson et al. 1977; Minns 1981; Marshall and Ryan 1987), Secchi depth transparency (Johnson et al. 1977; Kelso et al. 1986; Marshall and Ryan 1987), surface area (Marshall and Ryan 1987), and elevation (Kelso et al. 1986). Water depth appears to be the most critical of these physical variables. Lake trout lakes generally have mean depths greater than 6 m (Johnson et al. 1977; Marshall and Ryan 1987). Marshall and Ryan (1987) suggested that such depths are necessary for thermal stratification to occur. Lake trout are usually restricted to lakes that stratify in summer and have cool, well-oxygenated hypolimnetic waters.

In an extensive review of the literature on the effects of acidification, Baker et al. (1988) concluded that pH was the most useful predictor variable of lake trout presence and that a "critical threshold" of pH 5.5–5.3 existed below which lake trout populations declined to extinction. Our findings indicate that further improvements in predictive ability can be achieved by using a combination of common variables (pH, alkalinity, conductivity) instead of pH alone. Use of this PCA factor score may also reduce some of the problems related to seasonal and diurnal variability in lake water pH because alkalinity and conductivity are relatively stable parameters.

Lake trout is considered an important indicator species with respect to the health of the fragile aquatic ecosystems that it inhabits (Behnke 1972; Ryder and Johnson 1972). The simple predictive relationships provided by this study should aid managers in assessing the effects of future changes in acid deposition on lake trout resources. Additional indices will no doubt be needed to assess the effects of other anthropogenic stresses.

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References

Baker, J. P., D. P. Bernard, S. W. Christenson, and M. J. Sale. 1990. Biological effects of changes in surface water acid–base chemistry. State of Science/Technol. Rep. 13, Natl. Acid Precip. Assess. Program. Report for the U.S. Environmental Protection Agency, Corvallis, OR.

Baker, J. P., C. S. Creager, W. Warren-Hicks, S. W. Christensen, and L. Godbut. 1988. Identification of critical values for effects of acidification on fish populations. Final Project Report to the U.S. Environmental Protection Agency, Corvallis, OR.

Beamish, R. J. 1972. Design of a trapnet for sampling shallow-water habitats. Fish. Res. Board Can. Tech. Rep. 305: 14 p.

1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. Water Air Soil Pollut. 6: 501–514.

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

Beggs, G. L., and J. M. Gunn. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711–717.

Beggs, G. L., J. M. Gunn, and C. H. Olver. 1985. The sensitivity of Ontario lake trout (*Salvelinus namaycush*) and lake trout lakes to acidification. Ont. Fish. Tech. Rep. Ser. No. 17: 24 p.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. 29: 639–671.

Carl, L., M.-F. Bernier, W. Christie, L. Deacon, P. Hulsman, D. Loftus, D. Maraldo, T. Marshall, and P. Ryan. 1990. Fish community and environmental effects on lake trout. Lake Trout Synthesis, Ontario Ministry of Natural Resources, Toronto, Ont. 47 p.

Casselman, J. M., and H. H. Harvey. 1973. Fish traps of clear plastic. Prog. Fish-Cult. 35: 218–221.

Dixit, A. S., S. S. Dixit, and J. P. Smol. 1992. Long-term trends in lake water pH and metal concentrations inferred from diatoms and chrysophytes in three lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 17–24.

Dixit, S. S., A. S. Dixit, and J. P. Smol. 1989. Lake acidification recovery can be monitored using chrysophycean microfossils. Can. J. Fish. Aquat. Sci. 46: 1309–1312.

Dodge, D. G., G. A. Goodchild, I. MacRichie, J. C. Tilt, and D. G. Waldriff. 1985. Manual of instructions: aquatic habitat inventory surveys. Ontario Ministry of Natural Resources, Toronto, Ont. 169 p.

Evans, D. O., B. A. Henderson, N. J. Bax, T. R. Marshall, R. T. Oglesby, and W. J. Christie. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 448–470.

Fraser, J. M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. Trans. Am. Fish. Soc. 107: 505–517.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York, NY. 257 p.

Green, D., J. Matuszek, and D. Wales. 1987. Extensive survey data report. Ont. Fish. Acid. Rep. Ser. No. 87-12: 89 p.

Gunn, J. M., J. G. Hamilton, G. M. Booth, C. D. Wren, G. L. Beggs, H. J. Rietveld, and J. R. Munro. 1990. Survival, growth, and reproduction of lake trout (*Salvelinus namaycush*) and yellow perch (*Perca flavescens*) after neutralization of an acidic lake near Sudbury, Ontario. Can. J. Fish Aquat. Sci. 47: 446–453.

Harvey, H. H., and C. Lee. 1982. Historical fisheries changes related to surface water pH changes in Canada, p. 45–55. *In* R. E. Johnson [ed.] Acid rain fisheries. American Fisheries Society, Bethesda, MD.

Holtze, K. E., and N. J. Hutchinson. 1989. Lethality of low pH and Al to early life stages of six fish species inhabiting precambrian shield waters in Ontario. Can. J. Fish. Aquat. Sci. 46: 1188–1202.

Hutchinson, N. J., K. E. Holtze, J. R. Munro, and T. W. Pawson. 1989. Modifying effects of life stage, ionic strength and post-exposure mortality on lethality of H^+ and Al to lake trout and brook trout. Aquat. Toxicol. 15: 1–26.

Johnson, D. W., H. A. Simonin, J. R. Colquhuon, and F. W. Flack. 1987. *In situ* toxicity tests of fishes in acid water. Biogeochemistry 3: 181–208.

Johnson, M. G., J. H. Leach, C. K. Minns, and C. H. Olver. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui*). J. Fish. Res. Board Can. 34: 1592–1601.

Keller, W., and J. R. Pitblado. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

Keller, W., J. R. Pitblado, and J. Carbone. 1992. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 25–32.

Kelso, J. R. M., C. K. Minns, J. E. Gray, and M. L. Jones. 1986. Acidification of surface waters in eastern Canada and its relationship to aquatic biota. Can. Spec. Publ. Fish. Aquat. Sci. 87: 42 p.

Kitchell, J. F., and S. R. Carpenter. 1987. Piscivores, planktivores, fossils and phorbins, p. 132–146. *In* W. C. Kerfoot and A. Sih [ed.] Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Krester, W., J. Gallagher, and J. Nicoletter. 1989. Adirondack Lakes Study 1984–1987: an evaluation of fish communities and water chemistry. Adirondack Lakes Survey Corporation, Ray Brook, NY.

Marshall, T. R., and P. A. Ryan. 1987. Abundance patterns and community attributes of fishes relative to environmental gradients. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 198–215.

Martin, N. V., and C. H. Olver. 1976. The distribution and characteristics of Ontario lake trout lakes. Ont. Minist. Nat. Resour. Fish Wildl. Res. Rep. 97: 30 p.

Matuszek, J. E., and G. L. Beggs. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

MATUSZEK, J. E., J. GOODIER, AND D. L. WALES. 1990. The occurrence of Cyprinidae and other small fish species in relation to pH of Ontario lakes. Trans. Am. Fish. Soc. 119: 850–861.

MATUSZEK, J. E., AND D. L. WALES. 1990. The status of lake trout, brook trout, smallmouth bass, and walleye populations in Ontario with respect to acidification. Ont. Fish. Acid. Rep. Ser. No. 90-16.

MATUSZEK, J. E., D. L. WALES, AND J. M. GUNN. 1992. Estimated impacts of SO_2 emissions from Sudbury smelters on Ontario's sportfish populations. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 87–94.

MCQUEEN, D. J., M. R. S. JOHANNES, J. R. POST, T. J. STEWART, AND D. R. S. LEAN. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59: 289–309.

MILLS, K. H., S. M. CHALANCHUK, L. C. MOHR, AND I. J. DAVIES. 1987. Responses of fish populations in Lake 223 to 8 years of experimental acidification. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 114–125.

MILLS, E. L., AND A. SCHIAVONE, JR. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake production. N. Am. J. Fish. Manage. 2: 14–27.

MINNS, C. K. 1981. Acid rain: a preliminary estimate of the risk to Ontario's inland fisheries. Can. MS Rep. Fish. Aquat. Sci. 1622.

NEARY, B. P., P. J. DILLON, J. R. MUNRO, AND B. J. CLARK. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ont. Minist. Environ. Rep., Toronto, Ont. 170 p.

OLVER, C. H., R. L. DESJARDINE, C. I. GODDARD, M. J. POWELL, H. J. RIETVELD, AND P. D. WARING. 1990. Lake trout in Ontario: management strategies. Lake Trout Synthesis, Ontario Ministry of Natural Resources, Toronto, Ont. 90 p.

OMOE (ONTARIO MINISTRY OF THE ENVIRONMENT). 1981. Outline of analytical methods. MOE, Toronto, Ont. 246 p.

RAHEL, F. J. 1986. Biogeographic influences on fish species composition of northern Wisconsin lakes with applications for lake acidification studies. Can. J. Fish. Aquat. Sci. 43: 124–134.

RMCC. 1990. The 1990 Canadian long-range transport of air pollutants and acid deposition report: aquatic effects. Federal/Provincial Research and Monitoring Coordination Committee (RMCC) Rep. 4, Department of Fisheries and Oceans, Burlington, Ont. 151 p.

RYDER, R. A., AND L. JOHNSON. 1972. The future of salmonid communities in North American oligotrophic lakes. J. Fish. Res. Board Can. 29: 941–949.

SCHOFIELD, C. L., AND C. T. DRISCOLL. 1987. Fish species distribution in relation to water quality gradients in the North Branch of the Moose River Basin. Biogeochemistry 3: 63–85.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 382 p.

SPSS. 1986. SPSS^x user's guide: statistics, version 3 edition. SPSS Inc., Chicago, IL.

TONN, W. M., AND J. J. MAGNUSON. 1982. Patterns of species composition and richness in fish assemblages in northern Wisconsin lakes. Ecology 63: 1149–1166.

Dynamics in Year-Class Strength, Growth, and Calcified-Structure Size of Native Lake Trout (*Salvelinus namaycush*) Exposed to Moderate Acidification and Whole-Lake Neutralization

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Accurate age-interpretation techniques were developed, using scales and otoliths, to examine the role of whole-lake neutralization in the resurgence of a lake trout (*Salvelinus namaycush*) fishery in Nelson Lake (pH 5.7) near Sudbury, Ontario. Calcified structures and data from 860 lake trout were collected from 1972 to 1987. The population was characterized by the regular cyclic occurrence of strong year classes, which were probably an effect of pulse angling, cyclic food abundance, and possibly intraspecific interaction. The majority (65.8%) of the lake trout caught in the exceptional winter fishery of 1980 (3.3 $kg \cdot ha^{-1}$) were in the lake prior to liming in 1975–76. Young lake trout (up to age 4) of the 1975 and 1976 year classes grew bigger and had larger scales than other year classes from 1973 to 1977, coinciding with an increase in hypolimnetic zooplankton, probably related to improved water quality. Otoliths grew significantly larger and more translucent and exceeded relative growth of scales and body for all ages in 1976 (18% greater) and for the 1976 year class, confirming that otolith accretion can come from the ambient water because liming increased the calcium content by 33% that year, the only observed direct effect of the treatment.

Des techniques précises d'interprétation de l'âge ont été mises au point, à l'aide d'écailles et d'otolithes, pour examiner le rôle de la neutralisation à l'échelle du lac dans la réapparition d'une pêcherie de touladi (*Salvelinus namaycush*) dans le lac Nelson (pH 5,7) près de Sudbury (Ontario). Entre 1972 et 1987, les structures calcifiées et les données relatives à 860 touladis ont été recueillies. La population était caractérisée par l'apparition régulière et cyclique de classes d'âge robustes, qui étaient probablement un effet des variations cycliques de la pêche sportive, de l'abondance cyclique des aliments et peut-être d'interactions intraspécifiques. La majorité (65,8 %) des touladis capturés dans la pêcherie d'hiver exceptionnelle de 1980 (3,3 $kg \cdot ha^{-1}$) se trouvaient dans le lac avant le chaulage effectué entre 1975 et 1976. Les touladis jeunes (jusqu'à l'âge de 4 ans) des classes d'âge 1975 et 1976 sont devenus plus grands et ont eu des écailles plus grandes que ceux des autres classes d'âge entre 1973 et 1977, période coïncidant avec une augmentation du zooplancton hypolimnique, probablement en raison de l'amélioration de la qualité de l'eau. Les otolithes sont devenus beaucoup plus grands et plus translucides et leur croissance a été supérieure à la croissance relative des écailles et du corps, toutes classes d'âge confondues, en 1976 (18 % de plus) et pour la classe d'âge de 1976, ce qui confirme que les dépôts d'otolithes peuvent provenir de l'eau ambiante parce que le chaulage a augmenté la teneur en calcium de 33 % cette année-là, le seul effet direct observé du traitment.

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Whole-lake neutralization is widely used by fisheries managers to protect and restore sport fisheries adversely affected by acid deposition (Olem 1991). When used to treat severely degraded lakes where fish species have become extinct, lake neutralization has often proved to be an effective means of restoring a recreational fishery (Gloss et al. 1989; Gunn et al. 1990; Olem 1991). However, as a protective measure where indigenous fish communities still exist, the observed effects of base additions are highly variable (Howell et al. 1991; Porcella et al. 1991) and are generally unpredictable because of the confounding effects of other natural and anthropogenic factors.

Lake neutralization has been used experimentally in a small number of lakes in the Sudbury area (Yan and Dillon 1984; Keller et al. 1990), where emissions from local industries have caused extensive damage to sport fisheries, particularly lake trout (*Salvelinus namaycush*) fisheries (Beamish and Harvey 1972; Harvey and Lee 1982; Matuszek et al. 1992). In one of these lakes, Nelson Lake, a dramatic expansion in the lake trout fishery occurred after liming (Gunn et al. 1988). A variety of factors from changes in background deposition of acid and metals (Keller and Pitblado 1986; Keller et al. 1992) to shifts in prey species (Yan et al. 1977a; Gunn et al. 1988) and fluctuations in angling effort were alternative explanations for the improved fishery after liming (Gunn et al. 1988).

We used detailed examination of scales, otoliths, and other calcified tissues and measures of year-class strength before and after liming to determine (1) the role of liming in the expanded

TABLE 1. Selected chemical and biological characteristics of Nelson Lake, 1973–87. All water samples were collected during the ice-free period. Note the changes in sampling methods described in the footnotes. Catch-per-unit-of-effort (CPUE) is indicated for three common littoral zone fish species. CPUE is the mean number of fish captured during 24-h sets of fine-mesh 4-ft trap nets, at six index netting sites (from Gunn et al. 1988).

	Chemical characteristics							Littoral fish community (CPUE)		
Year	pH	Alk. ($mg \cdot L^{-1}$)	Ca ($mg \cdot L^{-1}$)	SO_4 ($mg \cdot L^{-1}$)	Cu ($\mu g \cdot L^{-1}$)	Ni ($\mu g \cdot L^{-1}$)	Al ($\mu g \cdot L^{-1}$)	Yellow perch	Brown bullhead	Smallmouth bass
1973[a]	5.8	0.3	5.0	16.4	17	24				
1974[a]	5.6	0.2	4.4	16.1	29	18	78			
1975[b,d]	5.7	0.5	4.1	15.8	22	17	87	805	13	0
1976[b]	6.4	2.2	5.3	15.1	15	10	30	536	10	0
1977[b]	6.3	1.7	5.0	15.3	4	7	21	431	11	0
1978[b]	6.5	2.5	4.7	14.9	3	7	17	224	6	0.2
1979[b]	6.3	1.7	4.7	14.4	2	6	19	128	4	0
1980								22	2	4
1981[c]	6.7	1.5	3.8	11.5	4	6	28			
1982[c]	6.4	1.8	4.1	12.4	1	5	5			
1983[c]	6.5	1.6	3.6	12.4	2	4	27			
1984								19	1	2
1985[b]	6.4	1.5	3.3	11.8			17			
1986[b]	6.4	1.8	3.5	11.6			14			
1987								4	1	14

[a]Surface grab samples (data from Yan and Dillon 1984).
[b]Volume-weighted whole-lake composite (1975–79 data from Yan and Dillon 1984; 1985–86 data from W. Keller, unpubl.).
[c]Epilimnion/metalimnion tygon tube composite sample (W. Keller, unpubl.).
[d]Only data from the preneutralization period of 1975 included.

lake trout fishery of Nelson Lake and (2) whether the growth of the body and calcified structures of lake trout was affected by the chemical treatment. The study involved the development and application of accurate age-interpretation techniques for samples collected over a 16-yr period.

Study Lake

Nelson Lake (48°44′N, 81°05′W) is a deep, clear (8-m Secchi depth), oligotrophic lake (A_0 348 ha, $\bar{Z}$ 11.6 m, Z_{max} 51.0 m) located 28 km north of Sudbury, Ontario. It is accessible by road, and there are several cottages on the shoreline. Prior to the addition of lime, the lake was moderately acidic (pH 5.7) and had high levels of waterborne metals, indicating that it was affected by emissions from Sudbury smelters (Yan et al. 1977b). In the fall of 1975 (September 9–23) and the spring of 1976 (May 26–31), a total of 6.8×10^4 kg of $Ca(OH)_2$ and 5.1×10^4 kg of $CaCO_3$ was added to the lake (Scheider et al. 1976). The addition of lime increased the pH to 6.4 and increased the Ca concentration from 4.1 to 5.4 $mg \cdot L^{-1}$. Metals such as Cu, Ni, Al, and Zn declined substantially after liming (Table 1). There were no short-term changes in transparency, nutrient chemistry, or plankton assemblages (Yan and Dillon 1984). The lake did not reacidify after liming, but the Ca concentration steadily declined between 1976 and 1986 (Table 1). Dilution by precipitation and stream waters and reduced weathering action under less acidic deposition in recent years (Keller et al. 1992) are probably both responsible for the declining Ca concentration after liming (Table 1).

In the early 1970s, the fish community of Nelson Lake appeared to exhibit classic symptoms of acidification stress: lake trout fishing was poor and few anglers used the lake (Ontario Ministry of Natural Resources, Sudbury District, unpubl. data), smallmoth bass (*Micropterus dolomieu*), an acid-sensitive species, had become extinct, and yellow perch (*Perca flavescens*), an acid-tolerant species, dominated the littoral zone.

No mass mortality or other immediate effects on the fish community were detected at the time of liming. However, numbers of yellow perch began to decline rapidly (Table 1). Yellow perch catches at index netting sites declined by 235 times between 1975 and 1987 (Gunn et al. 1988). Other observed changes in the littoral zone community were a decline in brown bullhead (*Ameiurus nebulosus*) numbers and the reestablishment of a reproducing smallmouth bass population from fish stocked in 1978 (Gunn et al. 1988).

Angling pressure in Nelson Lake has been extremely variable over the years and influenced by angling success and to a considerable extent by anglers' hearsay and perceptions. Local fishermen have reported (J. M. Casselman, pers. comm.) that there was moderately heavy angling in 1964 and 1965 and that there was also an excellent winter fishery in 1970–71. However, few, if any, people fished the lake in 1975 and 1976. Angling pressure for lake trout increased in 1979 (4 yr after liming) and increased dramatically during the winter angling season of 1980. An estimated 28 137 h of fishing effort was exerted during the 3 mo of the winter 1980 season, and approximately 2132 lake trout were harvested (Gunn et al. 1988). This represented a winter angling harvest of lake trout of 3.3 $kg \cdot ha^{-1}$, one of the highest ever reported for an Ontario lake. Lake trout harvests for 87 Ontario lakes documented by Goddard et al. (1987) ranged from 0.01 to 1.90 $kg \cdot ha^{-1}$.

Materials and Methods

Samples

Calcified tissues and total length data from 860 lake trout collected over a 16-yr period were used in this study (Table 2). Most of the samples (81%) were obtained from anglers through creel surveys. The remaining samples were collected during experimental gillnet surveys described in Table 2. Scale samples were the most frequently collected tissue (98%), but samples of otoliths (14%) and other calcified structures (15%),

TABLE 2. Lake trout collections used in the present study. Numbers of fish sampled (*N*), scales, otoliths, and other calcified structures are indicated. Gill nets were composed of 15.2-m panels; total length of the nets set is indicated, along with the range of mesh sizes (stretch measurement). The type of gillnet set in 1972, 1974, and 1979 was not reported.

Year	Month	Collection gear	*N*	Scales	Otoliths	Other
1972	July	Experimental gill net	7	7		
1973	July	Experimental gill net	10	10		
1974	Aug.	Experimental gill net	9	9		
1975	May	Experimental gill net (305 m, 19–25 mm)	1	1		
1975	Oct.	Experimental gill net (243 m, 38–127 mm)	34	31		
1976	July	Experimental gill net (1241 m, 9–51 mm)	23	21		
1977	July	Experimental gill net (243 m, 38–127 mm)	59	59		
1978	May	Experimental gill net (305 m, 19–25 mm)	5	5		
1979	May	Creel survey, angling	45	45		
1979	Oct.	Experimental gill net	25	23	10	11
1980	Jan.	Creel survey, angling	218	218	16	16
1980	Feb.	Creel survey, angling	178	178	7	7
1980	Mar.	Creel survey, angling	51	51	2	2
1980	July	Creel survey, angling	11	3		
1980	July	Experimental gill net (305 m, 19–25 mm)	26	26		
1984	July	Experimental gill net (305 m, 19–25 mm)	20	20	20	20
1985	Apr.	Creel survey, angling	18	18	18	18
1985	May	Creel survey, angling	40	40	28	27
1985	June	Creel survey, angling	23	23	21	23
1985	July	Creel survey, angling	6	6		
1985	Aug.	Creel survey, angling	8	8		
1987	July	Experimental gill net (305 m, 19–25 mm)	31	31		
1987	July	Creel survey, angling	8	8		
Total			860	845	124	128

such as opercula, subopercula, cleithra, branchiostegal rays, and vertebral centra, were also collected from a small but representative sample of fish (Table 2).

Age Determination and Validation Procedures

Cellulose acetate imprints were made from at least four or five clean scales for each fish. Ages were interpreted from the scales at 64× magnification by enumerating the number of checks, or breaks, in the configuration of circuli that were complete and considered to be associated with annuli (Cable 1956; Casselman 1983, 1987). Age was assessed on all scale samples by two to four experienced interpreters. Calcified-structure age (CSA) was recorded for each sample, along with the interpreter's confidence rank (1, little or no confidence; 9, extremely confident). An edge code was used to distinguish between the current and the previous year's growth on the edge of the structure. If a check associated with the next annulus was on the edge, the structure was considered to be in the "o" condition. For a CSA that included the "o" condition, the number of completed annuli (NCA) is one less than the simple numerical value of the CSA. For most growth comparisons, only the NCA was used.

Since several interpretations existed for each scale sample, the modal NCA was used. If no consistent interpretation existed after repeated reexamination of the scale imprints, the interpretation with the highest confidence rank was used.

Otoliths were embedded in epoxy resin (Araldite, by Ciba-Geigy), and thin transverse sections were cut through the origin, or nucleus, at right angles to the long axis of the otolith. The section was then mounted on a glass slide and buffed and polished to a thickness of 305 ± 25 μm with aluminum oxide lapping film (Brothers 1987). Acetate replicates were made of the polished surface of the section after it was etched with 2% HCl for 50 s, dried, and imprinted under pressure on a thin piece of cellulose acetate softened with a drop of acetone. The acetate imprints were then mounted and examined at 100× magnification. Two interpreters independently assessed the CSA of the replicates. When their interpretations disagreed, independent interpretations (up to two) were conducted by one interpreter until there was agreement. As with the scales, if a modal interpretation (NCA) was not achieved, the interpretation with the highest confidence rank was used.

Age-interpretation terminology and methods for otoliths were similar to those used for scales except that in otoliths the annuli were associated with translucent zones in the transverse sections and with corresponding narrow translucent lamellae in the replicas.

Other calcified structures, especially the flat bones, were examined, and age was interpreted following the methods of Casselman (1974). The results of these interpretations are not presented in detail because they were used only for comparative purposes to support or contest interpretations made from scales and otoliths.

The validity of age interpretation was examined by evaluating the consistency with which strong year classes, when sampled in succeeding years, were correctly recognized.

Relative Year-Class Strength

Year class, or year of hatch, was calculated for each fish, using the NCA and the edge condition. Edge condition was used to determine, depending on date of capture, whether the growth on the edge of the structure was from the current or previous season. Year class was assigned to all interpretations that were considered to be reliable. Relative year-class strength was calculated as the percent frequency of individual year classes among all samples of fish collected during the study period. The 1980 winter samples were excluded from this measure of relative year-class strength because of the atypically

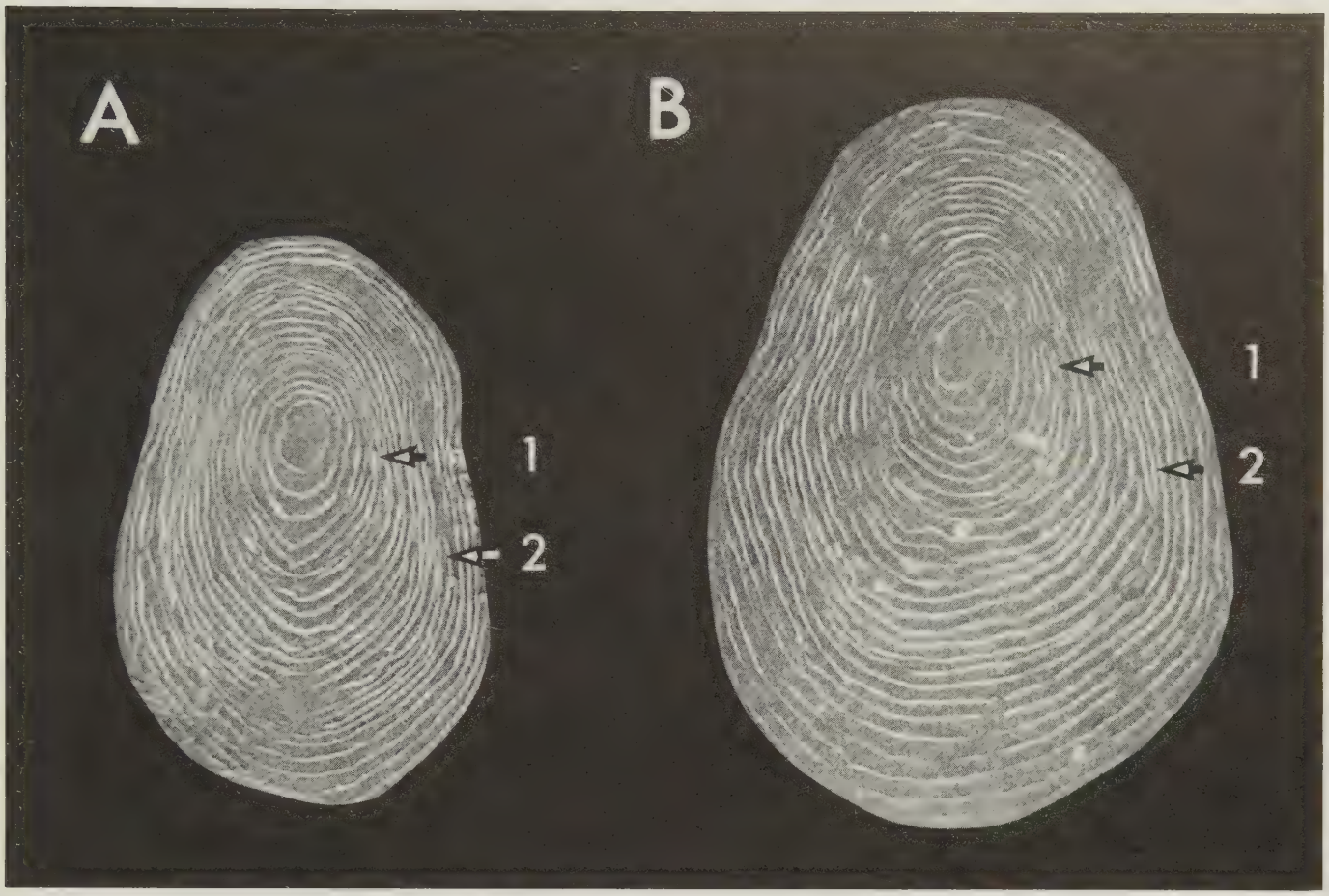

FIG. 1. Age interpretations of typical scales of two young lake trout taken in fine-mesh gill nets set in deep water in Nelson Lake. (A) July 24, 1977, 14.0 cm TL and 23.3 g total weight (TW); (B) July 22, 1977, 18.3 cm TL and 44.4 g TW. Both scales were interpreted to have two annuli, indicated by arrows. Scale ages were assessed as 3o (from the 1975 year class), indicating that a check was on the edge (''o'' condition), which would be associated with the next annulus. The annuli are associated with fragmented circuli that are thin and narrowly spaced in the case of the first annulus. Magnification 52×.

large number of fish captured by anglers during that period. The 1980 winter samples were excluded only when it was shown that the distributions of selected year classes (1972–1977) were not significantly different ($\chi^2 = 3.28$, df = 5, $P = 0.66$) between the 1975 and 1980 gillnet samples and the 1980 winter angling samples.

Length Frequency, Length at Age, and Growth

Length–frequency distributions were prepared using 5-cm length classes. Modal age and year class were assigned to the most prominent length modes, which, when compared across years, indicated changes in linear body size, or growth. Body-size-at-age comparisons were made, using three age groups (3, 4, and 5) from the three major sampling periods, and von Bertalanffy growth equations were calculated from mean body length at CSA. Results were not separated by sex because body growth of lake trout is not usually sexually dimorphic within the size and age range of most fish in this study (J. M. Casselman, unpubl. data).

Absolute and Relative Otolith and Scale Size

Precise measurements were made of otoliths and scales to assess changes in the size of these tissues after lake liming. Otolith measurements were made from the acetate replicas at 58.6× magnification. Measurements were made from the origin (nucleus) to each annulus along the maximum ventral radius of the otolith section. The measurement was precisely located at the distal edge of the translucent lamella associated with the annulus. Measurements were performed with a digitizing tablet and computer interfaced with a microscope fitted with a camera lucida.

Scales were measured only for samples that also had otolith age interpretations. Unlike otoliths, where all annuli were measured, only the first four scale checks that were considered to be associated with annuli were measured because scale age interpretations for older fish were unreliable. The scale image was projected on the digitizing tablet using a microfische reader and a mirror-mounted projection stand and measured along the maximum anterior radius at 64.0× magnification.

The difference in the distance between two adjacent annuli was calculated to determine the annual incremental scale and otolith growth for a specific year and growing season. Otolith age interpretations were used to assign year class. This made it possible to assign the annual incremental scale growth for the first 4 yr to specific years even though ages interpreted from the scales of older fish were inaccurate. For general comparisons among year classes, the sizes for the first four annual increments were combined and compared with the overall mean for the period.

Regression analysis was used to determine whether significant correlations existed between the relative abundance of var-

FIG. 2. Age interpretation of a typical scale from an older lake trout angled from Nelson Lake January 16, 1980 (40.6 cm TL, 500 g TW, female). The first annulus is associated with numerous thin, narrowly spaced, fragmented circuli; the second and third annuli are associated with less distinct checks involving more uniformly spaced and thicker circuli. Arrows indicate three distinct annuli. Scale age was assessed as 4o (from the 1976 year class). Magnification 52×.

ious year classes of lake trout in Nelson Lake and the relative size of the annual incremental growth of otoliths and scales during the period 1975–85.

Results

Age Determination and Validation

Checks on the scales were quite distinct in the younger fish. The first few checks that were considered to be associated with annuli were closely spaced and relatively distinct, with narrow, fragmented circuli (Fig. 1). Generally, the next few scale checks associated with annuli were less distinct and more difficult to locate (Fig. 2) and were usually composed of wider spaced circuli that were uniformly spaced but somewhat discontinuous and fragmented. The more distal checks on the scales were extremely difficult to resolve because they coalesced, indicating that annual scale growth of fish over approximately age 6 was greatly reduced. Multiple interpretations for older fish showed considerable variability in that the circuli on the edge of the scale were fragmented and discontinuous, making it impossible to either recognize or locate distal annuli consistently.

Zonation in the acetate replicas of the otolith sections was relatively distinct and easy to interpret (Fig. 3). The greatest difficulty involved recognizing and precisely locating the translucent zone considered to be associated with the first few annuli. The first annulus on the replicas was usually a considerable distance from the nucleus, indicating that the first annual growth zone in the otolith was much greater than

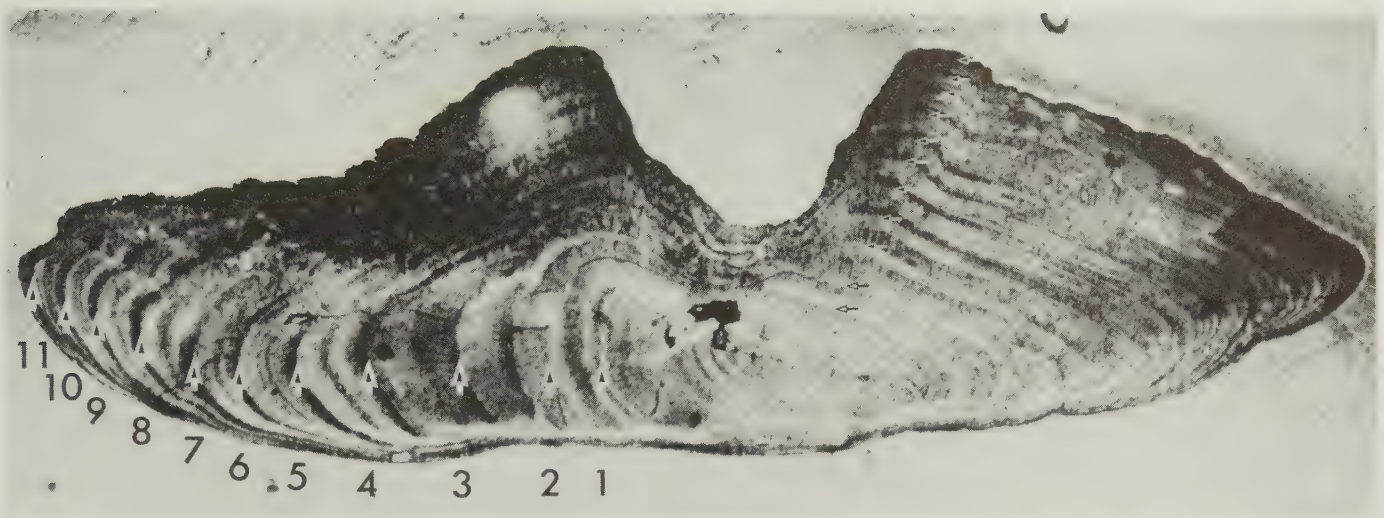

FIG. 3. Age interpretation of a typical acetate replica of a transverse otolith section from an older lake trout gillnetted October 5, 1979 (65.9 cm TL, 2600 g TW, male). Large arrows in the ventral region indicate 11 translucent zones associated with annuli, each just proximal to an opaque zone. The corresponding annuli are marked in the medial dorsal anterior region by small arrows. Acetate replica age was interpreted as 11+ (from the 1968 year class), indicating that there is opaque tissue on the edge ("+" condition), which was considered to be growth from the current year. Magnification 61×.

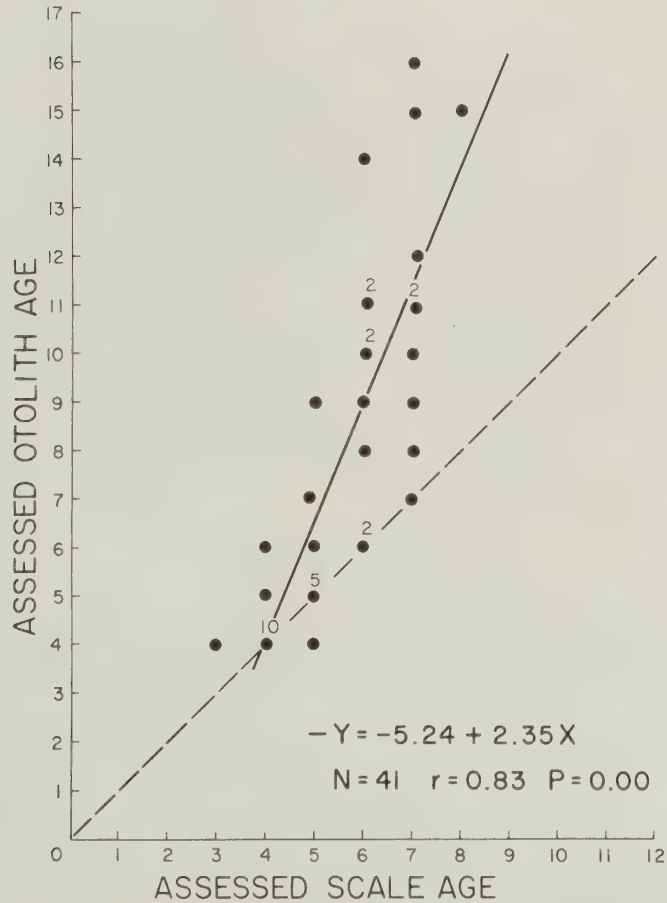

FIG. 4. Relationship between assessed otolith age and assessed scale age for a sample of 41 lake trout from Nelson Lake, 1979, 1980, and 1984. The regression line and equation are indicated.

subsequent annual zones. However, subsequent zones were distinctly demarcated, and the annuli were easy to resolve and enumerate.

Scale interpretations were reliable only up to age 5. For older lake trout, there was a sharp divergence in the age interpretations from scales as opposed to otoliths (Fig. 4). The interpretations of the two structures deviated in a linear fashion. Ages interpreted from scales were only half the otolith interpretations in the oldest fish (Fig. 4). Variability between the two types of interpretations was directly related to the amount of disparity.

Interpretations from the five additional bones (opercula, subopercula, branchiostegal rays, cleithra, and vertebral centra) also corroborated the otolith interpretations. The modal assigned age for the bones agreed with 88% of the otolith interpretations but with only 42% of the scale interpretations. Since otolith and scale interpretations showed good agreement up to age 5, it was decided to use scale age if the assessment was less than 6 and otolith interpretations if the scale assessment was greater than or equal to 6. This combined interpretation was adopted because only scale samples had been collected for many of the younger fish (Table 2). The validity of ages assigned by this combined method was confirmed through our success in tracking various year classes and cohorts of lake trout in Nelson Lake through successive sampling periods (Fig. 5, 6).

Age interpretations from otoliths produced von Bertalanffy length-at-age growth correlations that were realistic relative to the observed size of fish in the population. Otolith interpretations produced an L_∞ of 71.7 cm total length (TL) for the Nelson Lake population. Only one sampled lake trout (72.5 cm TL, 15o assessed age) exceeded this estimated utlimate length. By contrast, the estimated ultimate length (L_∞) from scales was 90.1 cm TL (Table 3), 25.7% greater than the largest fish sampled from the population.

Length Frequency, Length at Age, and Growth

Length–frequency distribution for samples from 1972 and 1980 indicated that during the early 1970s, progressively larger lake trout were taken by gill nets (Fig. 5). When modal ages were determined for the modal length classes, the general increase in body size of some of the major year classes could

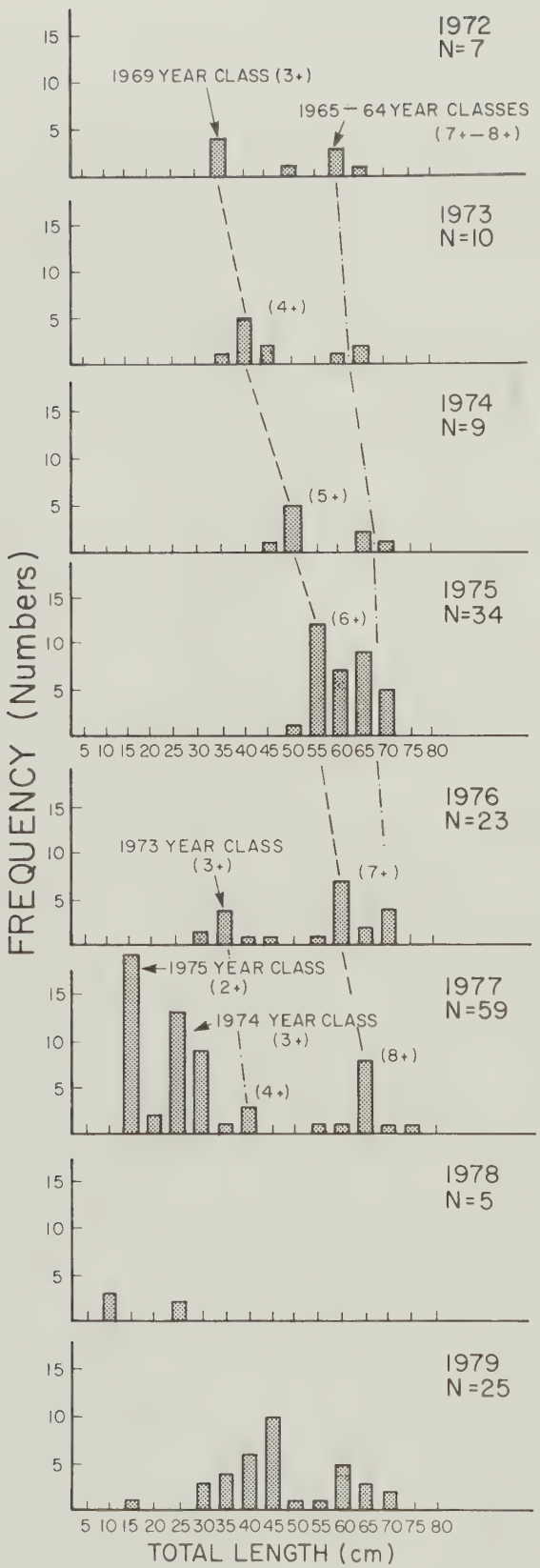

FIG. 5. Length–frequency distribution by year for 172 lake trout taken by gillnetting, 1972–79. The modal age and year classes for the modal length classes are indicated, showing progression of the modal length class (growth) and associated major year classes, 1964, 1965, 1969, and 1973. Too few samples were collected in 1978 to track the modes into 1979.

be tracked over the years. At an assessed scale age of 3+, the 1969 year class in 1972 was larger (35- to 40-cm length–frequency mode) than the 1973 year class in 1976 (30- to 35-cm mode), and both were larger than the 1974 and 1976 year classes in 1977 and 1980 (20- to 30-cm and 25- to 30-cm modes, respectively). Therefore, from the early to mid-1970s, young lake trout decreased in size.

Enough samples existed for fish of ages 3, 4, and 5 to allow an examination of changes in empirical body length at age throughout the study period. For lake trout of age 5, the 1970 and 1979 year classes were larger (+12.4 and +2.9%, respectively), and the 1968 and 1974 year classes were smaller (−8.1 and −7.2%, respectively) than the mean length at this age. In relation to liming, lake trout aged 3 and 4 for the 1975 and 1976 year classes were larger (+12.4 and +4.2%, respectively) whereas the 1973, 1974, and 1977 year classes from before and after the treatment were smaller (−8.0, −5.2, and +3.4%, respectively) than mean lengths at these two ages.

Relative Year-Class Strength

Year-class strength fluctuated in a distinctive cyclic pattern in Nelson Lake. Three cohorts, each composed of three year classes, were evident among the 21 year classes represented in this study. The cohorts exhibited modes in 1969, 1975, and 1981 (Fig. 6). There was some evidence of a fourth cohort during 1963–65; however, we had too few samples for very old fish from Nelson Lake to substantiate this observation.

Correlations among the relative strengths of various year classes were examined over the 11 yr for which there were adequate data (Table 4). Four highly significant ($P < 0.01$) correlations were detected. The relative size of a specific year class was negatively correlated with the size of the year classes 2 and 3 yr earlier and positively correlated with the year classes 5 and 6 yr earlier (Table 4).

The very large cohort that occurred in the mid-1970s (Fig. 6) and later contributed heavily to the massive harvest in the winter of 1980 was initially thought to be related to liming. However, two of these three strong year classes actually appeared before treatment. The lake trout taken by anglers in that fishery had several prominent length modes (Fig. 7). The largest, the 40- to 45-cm length class, were from the 1974 year class, the year before liming commenced.

Absolute and Relative Otolith and Scale Size

Otolith growth, particularly the first year's growth, also exhibited a cyclic pattern that peaked in the mid-1970s. However, liming appeared to have a direct effect on this measure. Otolith growth during the year of liming (1976) and the subsequent year (1977) was significantly greater than during the preceding 5 and succeeding 7 yr (Fig. 8). In 1976, this difference existed regardless of age and exceeded the largest possible estimated size (95% confidence limits) for the entire period by an average of 18.8%. The 1976 growth zone was usually more translucent than adjacent zones. The increase in 1977 was less (6.1%) and involved only the younger ages (1–3 and 5). Otolith increments were also significantly larger in 1975 for fish in their first year and in 1978 for fish in their second year (Fig. 8).

Scale growth was much more variable than otolith growth, but both structures exhibited a similar cyclic pattern in growth during the study period (Fig. 9). The relationship between scales and otolith growth and year-class strength (i.e. index of lake trout abundance) was complicated but appeared to be correlated with the size of both the preceding and succeeding year

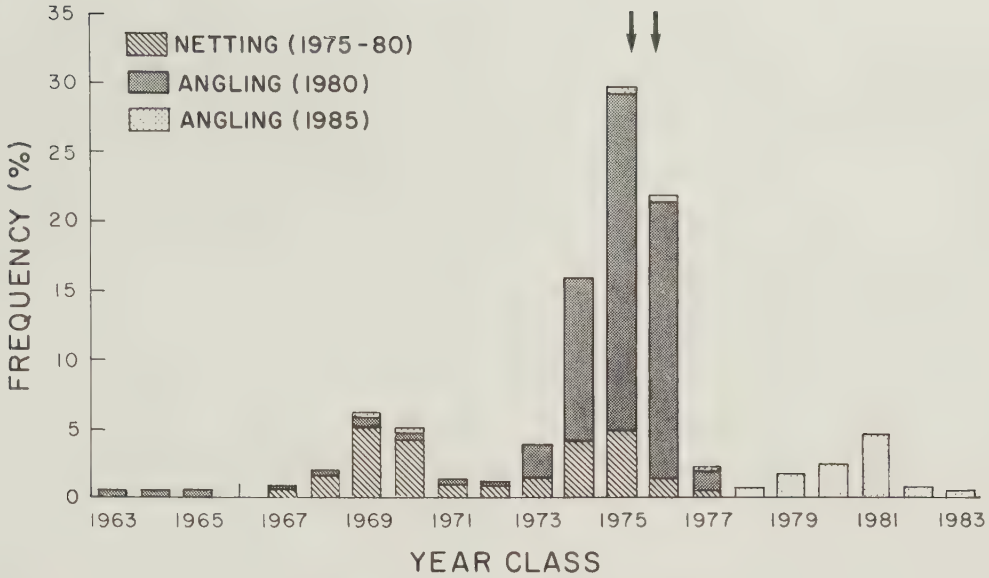

FIG. 6. Percent frequency of occurrence of various year classes of 638 lake trout, aged 3 and older, from a 21-yr period, 1963–83. Samples were taken by gillnetting (1975–80, $N = 122$) and angling (1980, $N = 447$; 1985, $N = 69$) from Nelson Lake. Arrows indicate the addition of lime: September 1975 and May 1976.

TABLE 3. Mean total length at age interpreted from scales and otoliths for a set of 101 lake trout taken from October to June in 1979, 1980, and 1985. Mean size of lake trout age 1 and 2 was obtained from back-calculated length at age for an additional sample of 5 and 29 fish, respectively (mean TL ± 95% confidence interval (CI) = 10.6 ± 0.4 and 16.9 ± 0.4), gillnetted in July; age and length at age were determined from scale interpretations and measurements. All other samples were taken from fish at either the beginning or end of the growing season, when the calcified tissue was in the growth cessation that would be associated with formation of the check or zone related to the annulus ("o" condition).

	Scale interpretations			Otolith interpretations		
Age	*N*	Mean TL (cm)	95% CI	*N*	Mean TL (cm)	95% CI
1	5	8.6	0.4	5	8.6	0.4
2	29	15.4	0.3	29	15.4	0.3
3	10	26.0	0.6	10	23.7	0.4
4	13	28.5	0.9	12	29.1	0.6
5	27	39.6	1.2	26	37.8	0.8
6	21	45.1	5.6	18	40.9	1.1
7	12	59.5	4.9	10	43.8	2.3
8	9	68.2	6.7	7	60.7	4.7
9	9	66.5	8.4	3	66.2	
10				4	66.7	
11				5	65.8	
12				1	63.0	
13				1	66.0	
14						
15				2	67.5	
16				1	71.6	
17				1	71.1	
von Bertalanffy coefficients						
L_∞		90.1			71.7	
k		0.167			0.211	
t_0		0.963			0.947	

classes (Table 4). The relative size of the calcified structure of a year class was positively correlated with the size of the preceding year class and negatively correlated with the size of the year class 4 yr before and 3 yr after. There was a negative correlation between the relative size of the structure and the accumulated size of the following three year classes (Table 4).

Relative growth of calcified structures was more extreme for scales than for otoliths in all years except 1976, the second year of lime treatment (Fig. 9). In 1976, the growth of otoliths was significantly greater than that of the scales, possibly because of the increased availability of Ca.

Discussion

Accurate age-interpretation techniques developed for this study allowed us to detect the cyclic nature of the lake trout population structure in this experimental lake. Such historic information was otherwise lacking for the premanipulation state of the Nelson Lake lake trout population, a situation not uncommon in many similar experiments (Peters 1991).

Because the majority of the samples were collected at approximately 5-yr intervals, which generally coincided with the frequency of occurrence of the most abundant year classes (5–6 yr), it might be suggested that relative year-class strength in this study is an artifact of sampling frequency. However, this assumption is not consistent with the results. Each set of samples usually contained strong year classes from at least two different cohorts, and these year classes persisted throughout the overall sampling period, confirming that relative year-class strength over the 21-yr period encompassed by the study was cyclic and dominated by regularly occurring strong cohorts (Fig. 6).

It seems quite unlikely that liming had much effect on year-class strength because most of the fish associated with the strong 1974–76 cohort predated liming. It is possible that survival of this cohort was somewhat enhanced by the chemical treatment because there was a coincident increase in body and calcified-structure growth. Nevertheless, the majority of the fish taken during the winter fishery of 1980 (68.2%) were not produced

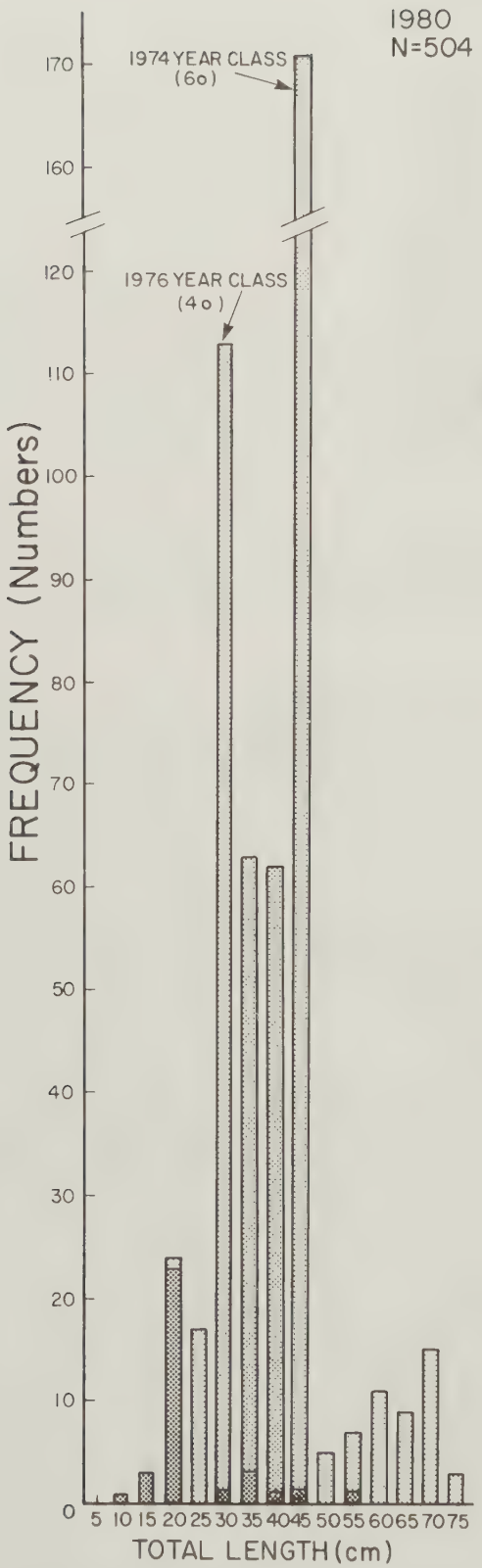

FIG. 7. Length–frequency distribution of 504 lake trout taken in 1980 by angling in the winter (light shading) and gillnetting in the summer (dark shading). The modal ages and year classes are indicated for the modal length classes. Otolith interpretations confirmed that the modal length class of 70 cm contained fish from the 1964 and 1965 year classes.

by liming but were associated with regular cyclic occurrence of successively strong year classes.

The lake trout population in Nelson Lake exhibited rather classic stock/recruitment relationships (Ricker 1975), with recruitment directly related to size of the spawning stock. There was a significant positive correlation between year-class strength and the strength of year classes 5–6 yr earlier (Table 4), an interval that coincides with the age of first maturity of lake trout populations in many lakes (Scott and Crossman 1973). Angling pressure, in turn, probably had a major effect on the size of the brood stock. This readily accessible lake near a large urban area was subject to highly variable fishing pressure (K. Lynn, area conservation officer, pers. comm.). Interviews with local anglers indicated that word-of-mouth information, particularly the suggestions by local baitfish dealers, influenced where fishing pressure was directed in particular years (J. Gunn, unpubl. information). Such socioeconomic factors are difficult to quantify (Eshenroder 1987), but we believe that they had a profound influence on angling pressure and harvest of adult lake trout from Nelson Lake.

Changes in the deposition of acid and metals from Sudbury smelters during the study period make it difficult to detect any direct effects of lake neutralization. The steady decline in industrial emissions during the 1960s and 1970s has led to widespread improvement in water quality in Sudbury area lakes (Keller et al. 1992). Some biological recovery has also been documented in lakes that have not been limed (Keller and Yan 1991; Keller et al. 1992). In one of these lakes that recovered naturally, a change in the fish community analogous to that of Nelson Lake occurred (increase in lake trout, decline in yellow perch) as the lake increased in pH from 5.4 (1980) to 5.9 (1988) (Gunn and Keller 1990). Nelson Lake, with an initial pH of 5.7, was above the toxic threshold for lake trout (pH 5.5, Beggs and Gunn 1986), but the decline in SO_4 levels in Nelson Lake both before and after liming (Table 1) is evidence that this lake was also responding to declining acid inputs. In addition, two hypolimnetic zooplankton species (*Daphnia longiremis, Cyclops scutifer*) first appeared in Nelson Lake in 1975 (Yan et al. 1977b; N. D. Yan and W. Keller, unpubl. data), just prior to liming.

Scales of young lake trout of year classes associated with liming grew faster, coincident with an increase in body growth. This we believe resulted from an increase in available food. Since juvenile lake trout, which live in deep water, are planktivorous (J. M. Casselman, unpubl. data), an increase in hypolimnetic zooplankters would explain the increase in body and scale growth in the 1976 year class. In another lake, increased zooplankton (*Mysis*) production after liming has been associated with increased growth of lake trout (Howell et al. 1991). However, in Nelson Lake, the combined effects of liming and reduced deposition of acids presumably contributed to the water quality improvements that allowed species such as *D. longiremis* to become established and to proliferate in the mid-1970s.

The typical growth pattern of scales and otoliths, with scale growth being more extreme than otolith growth (Casselman 1990), was exhibited for all year classes except the postneutralization year class of 1976. Otolith growth relative to body growth has been shown to be negatively allometric during rapid growth and positively allometric during slow growth (Secor et al. 1989; Casselman 1990). Otolith growth in 1976 was atypical, exceeding scale and body growth. Indeed, increased growth of the otoliths was the only effect that we could attribute directly to the whole-lake addition of Ca. Otoliths are com-

TABLE 4. Significant correlations between the relative strengths of various year classes and the relative size of the calcified structures (otoliths and scales) of various year classes of lake trout from Nelson Lake for an 18-yr period from 1966 to 1983. The relative size of the year class was expressed as a percent of the overall contribution for the entire period, excluding the excessive numbers obtained by anglers during the winter of 1980. The relative size of the calcified structures was expressed as the percent deviation from mean size for the 11-yr period, 1970–80.

	Relative size					
No.	Dependent variable *Y*	Independent variable *X*	Type of correlation	*N*	*r*	*P*
1	*N*th year class	*N*th − 2 year class	−	16	0.56	0.011
2	*N*th year class	*N*th − 3 year class	−	15	0.73	0.001
3	*N*th year class	*N*th − 5 year class	+	13	0.68	0.004
4	*N*th year class	*N*th − 6 year class	+	12	0.74	0.002
5	Calcified structures of *N*th year class	*N*th − 1 year class	+	11	0.83	0.001
6	Calcified structures of *N*th year class	*N*th − 4 year class	−	11	0.69	0.009
7	Calcified structures of *N*th year class	*N*th + 3 year class	−	11	0.86	0.000
8	Calcified structures of *N*th year class	Accumulated next three year classes	−	11	0.95	0.000

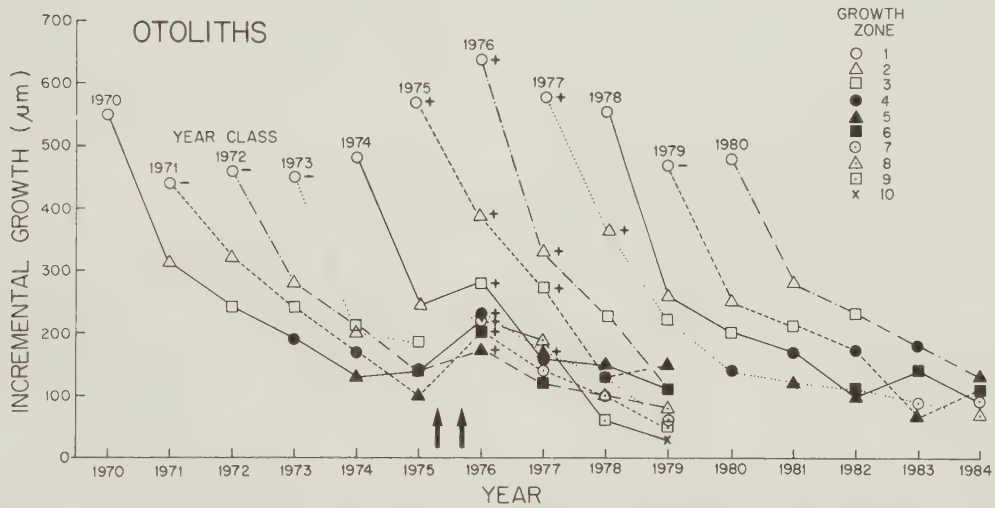

FIG. 8. Annual incremental otolith growth for 113 lake trout caught in Nelson Lake in 1979 and 1980 and also in 1984 and 1985, including 10 growth zones and 11 year classes encompassing a 15-yr period, 1970–84. Otolith increments deposited that were significantly larger or smaller than the overall mean (in relation to the 95% confidence limits) are indicated by + or −, respectively. Symbols depicting the various growth zones are illustrated and defined. Arrows indicate the addition of lime: September 1975 and May 1976.

posed of almost pure calcium carbonate (Casselman 1982) in the form of aragonite (Degens et al. 1969). Simkiss (1974) concluded that 90–98% of the Ca in fish came directly from the water. Ichii and Mugiya (1983) concluded that 85% of the Ca in goldfish (*Carassius auratus*) came from the aquatic environment. Irie et al. (1967) showed that otolith accretion can come directly from the water, and Solomatina and Grebenkina (1979) showed that Ca uptake in fish is proportional to its concentration in the surrounding water. Therefore, it is reasonable to assume that the 33% increase in Ca concentration in the water in 1976 (Yan et al. 1977b) as a result of whole-lake liming might have contributed to increased Ca deposition and translucency in the otoliths. Scales are much less calcareous (Casselman 1978), which probably explains why scale growth was less affected.

It was unexpected that the size of the calcified structures would be positively correlated with the strength of the previous year class (i.e. abundance) of lake trout in the lake. This seems paradoxical, given our general understanding of density-dependent growth. However, since year-class strength was cyclic during the period, cyclic growth may also have been driven by cycles in prey availability. For instance, in situations of high density of younger fish in the hypolimnion, cannibalism and a shift to piscivory in littoral species such as yellow perch may result in increased growth rate of omnivorous lake trout in spite of high intraspecific competition for zooplankton and zoobenthos. In subsequent years, continued cannibalism and competition among young lake trout in the deepwater nursery refugium could suppress younger recruits and subsequent year classes (Johnson 1976; Evans et al. 1991). This could account for our observation that the size of year classes of lake trout in Nelson Lake was inversely related to the size of year classes 2–3 yr earlier (Table 4).

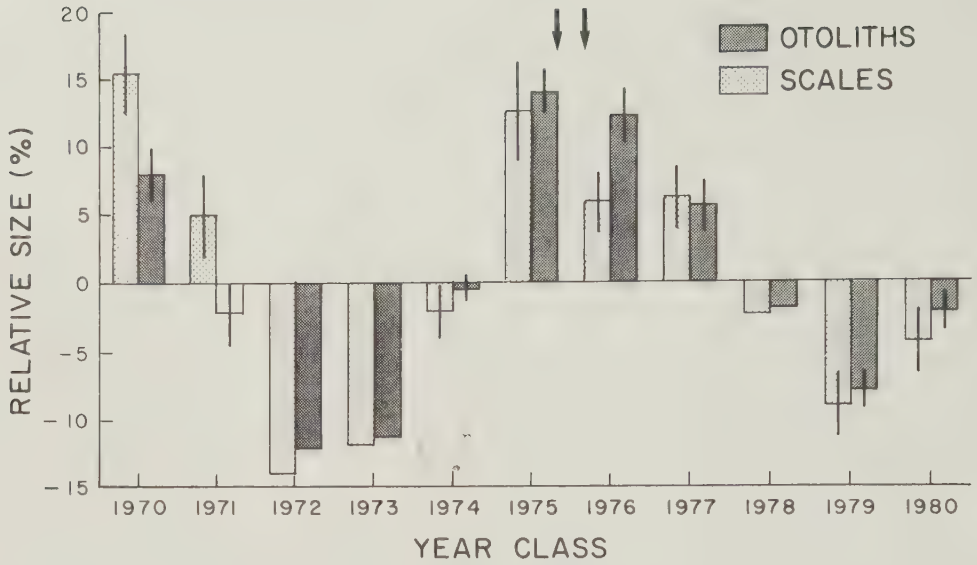

FIG. 9. Relative size of the otoliths and scales from the same lake trout (N = 95), for ages 1–4, from Nelson Lake for 11 year classes, 1970–80. Relative size is expressed as percent deviation from the overall mean for the period. Vertical bars indicate 95% confidence intervals where sample sizes were adequate (>5). Scale annuli were measured along the maximum anterior scale radius. Otolith age interpretations were used to assign year class. Arrows indicate the addition of lime: September 1975 and May 1976.

Overall, from 1963 to 1983, the Nelson Lake lake trout population underwent cyclic changes, probably driven by pulse angling pressure. The chemical conditions that existed both before and after this moderately acidic lake was limed appeared to have little or no direct mesurable effect on lake trout recruitment and population dynamics. However, liming directly affected otolith accretion and indirectly affected body and scale growth, probably through increased availability of zooplankton in the hypolimnion.

Acknowledgements

Many students and staff from the Ontario Ministry of Natural Resources, particularly Dana Cruikshank, assisted with the collection of lake trout samples. We thank the people who conducted age and growth interpretations of the calcified structures: Irene Weir conducted some of the early scale interpretations; Robert McLaughlin and Richard Strus interpreted scales, otoliths, and other calcified structures; Jon Tost examined otoliths; and Joe Dibbits interpreted and measured otoliths. The late Audrey Chui very capably drafted some of the figures. Constructive reviews of the manuscript were provided by Mike Jones, Bill Keller, Jim Reckahn, and two anonymous referees. This is contribution 92-06 of the Ontario Ministry of Natural Resources, Fisheries Branch, Research Section, Maple, Ont.

References

BEAMISH, R. J., AND H. H. HARVEY. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BEGGS, G. L., AND J. M. GUNN. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711–717.

BROTHERS, E. B. 1987. Methodological approaches to the examination of otoliths in aging studies, p. 319–330. *In* R. C. Summerfelt and G. E. Halls [ed.] Age and growth of fish. Iowa State University Press, Ames, IA.

CABLE, L. E. 1956. Validity of age determinations from scales, and growth of marked Lake Michigan lake trout. U.S. Fish Wildl. Serv. Fish. Bull. 107: 59 p.

CASSELMAN, J. M. 1974. Analysis of hard tissue of pike *Esox lucius* L. with special reference to age and growth, p. 13–27. *In* T. Bagenal [ed.] The ageing of fish — proceedings of an international symposium. Unwin Brothers, Old Woking, U.K.

1978. Calcified tissue and body growth of northern pike, *Esox lucius* Linneaus. Ph.D. thesis, University of Toronto, Toronto, Ont. 782 p.

1982. Chemical analyses of the optically different zones in eel otoliths, p. 74–82. *In* K. H. Loftus [ed.] Proceedings of the 1980 North American eel conference. Ont. Fish. Tech. Rep. Ser. No. 4.

1983. Age and growth assessment of fish from their calcified structures — techniques and tools. NOAA Tech. Rep. NMFS 8: 1–17.

1987. Determination of age and growth, p. 209–242. *In* A. H. Weatherley and H. S. Gill [ed.] The biology of fish growth. Academic Press, London.

1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119: 673–688.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH. 1969. Molecular structure and composition of fish otoliths. Mar. Biol. 2: 105–113.

ESHENRODER, R. L. 1987. Socioeconomic aspects of lake trout rehabilitation in the Great Lakes. Trans. Am. Fish. Soc. 166: 309–313.

EVANS, D. O., J. M. CASSELMAN, AND C. C. WILCOX. 1991. Effects of exploitation, loss of nursery habitat, and stocking on the dynamics and productivity of lake trout populations in Ontario lakes. Lake trout Synthesis, Response to Stress Working Group. Ontario Ministry of Natural Resources, Toronto, Ont. 193 p.

GLOSS, S. P., C. L. SCHOFIELD, R. L. SPATEHOLTS, AND B. A. PLONSKI. 1989. Survival, growth, reproduction, and diet of brook trout (*Salvelinus fontinalis*) stocked into lakes after liming to mitigate acidity. Can. J. Fish. Aquat. Sci. 46: 277–286.

GODDARD, C. I., D. H. LOFTUS, J. A. MACLEAN, C. H. OLVER, AND B. J. SHUTER. 1987. Evaluation of the effects of fish community structures on observed yields of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 239–248.

GUNN, J. M., J. G. HAMILTON, G. M. BOOTH, C. D. WREN, G. L. BEGGS, H. J. RIETVELD, AND J. R. MUNRO. 1990. Survival, growth, and reproduction of lake trout (*Salvelinus namaycush*) and yellow perch (*Perca flavescens*) after neutralization of an acidic lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 47: 446–453.

GUNN, J. M., AND W. KELLER. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

GUNN, J. M., M. J. MCMURTRY, J. M. CASSELMAN, W. KELLER, AND M. J. POWELL. 1988. Changes in the fish community of a limed lake near Sudbury, Ontario: effects of chemical neutralization or reduced atmospheric deposition of acids? Water Air Soil Pollut. 41: 113–136.

HARVEY, H. H., AND C. LEE. 1982. Historical fisheries changes related to surface water pH changes in Canada, p. 45–55. *In* R. E. Johnson [ed.] Acid rain/fisheries. American Fisheries Society, Bethesda, MD.

HOWELL, E. T., G. COKER, G. M. BOOTH, W. KELLER, N. NEARY, K. B. NICHOLLS, F. D. TOMASSINI, N. YAN, J. M. GUNN, AND H. REITVELD. 1991. Ecosystem responses of a pH 5.9 lake trout lake to whole lake liming, p. 61–95. *In* H. Olem, R. K. Scheiber, R. W. Brocksen, and D. B. Porcella [ed.] International lake and watershed liming practices. Terrene Inst., Washington, DC.

ICHII, T., AND Y. MUGIYA. 1983. Effects of dietary deficiency in calcium on growth and calcium uptake from the aquatic environment in the goldfish, *Carassius auratus*. Comp. Biochem. Physiol. 74A: 259–262.

IRIE, T., T. YOKOYAMA, AND T. YAMADA. 1967. Calcification of fish otolith caused by food and water. Bull. Jpn. Soc. Sci. Fish. 33: 24–26.

JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459–2488.

KELLER, W., D. P. DODGE, AND G. M. BOOTH. 1990. Experimental lake neutralization program: overview of neutralization studies in Ontario. Can. J. Fish. Aquat. Sci. 47: 410–411.

KELLER, W., J. M. GUNN, AND N. D. YAN. 1992. Evidence of biological recovery in acid stressed lakes near Sudbury, Canada. Environ. Pollut. 78: 79–85.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 285–296.

KELLER, W., AND N. D. YAN. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. 48: 1635–1644.

MATUSZEK, J. E., D. L. WALES, AND J. M. GUNN. 1992. Estimated impacts of SO_2 emissions from Sudbury smelters on Ontario's sportfish populations. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 87–94.

OLEM, H. 1991. Liming acid surface waters. Lewis Publ., Inc., Chelsea, MI.

PETERS, R. H. 1991. A critique for ecology. Cambridge University Press, New York, NY. 366 p.

PORCELLA, D. B., T. J. FAHEY, C. L. SCHOFIELD, C. T. DRISCOLL, R. M. NEWTON, D. J. RAYNAL, D. LEOPOLD, J. YAVITT, AND J. DEPINTO. 1991. Limestone treatment for management of aquatic and terrestrial ecosystems, p. 5–14. *In* H. Olem, R. K. Scheiber, R. W. Brocksen, and D. B. Porcella [ed.] International lake and watershed liming practices. Terrene Inst., Washington, DC.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SCHEIDER, W. A., J. JONES, AND B. CAVE. 1976. A preliminary report on the neutralization of Nelson Lake near Sudbury, Ontario. Ont. Minist. Environ. Tech. Rep. 36 p.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 382 p.

SECOR, D. H., J. M. DEAN, AND R. B. BALDEVARONA. 1989. Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. Rapp. P.-v. Réun. Cons. int. Explor. Mer 191: 431–438.

SIMKISS, K. 1974. Calcium metabolism of fish in relation to ageing, p. 1–12. *In* T. B. Bagenal [ed.] Ageing of fish. Unwin Brothers, Old Woking, U.K.

SOLOMATINA, V. D., AND T. G. GREBENKINA. 1979. Relation of the calcium level in fish tissues to its content in the water. Can. Transl. Fish. Aquat. Sci. 4552: 6 p.

YAN, N. D., AND P. J. DILLON. 1984. Experimental neutralization of lakes near Sudbury, Ontario, p. 417–456. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons, Toronto, Ont.

YAN, N. D., J. JONES, B. CAVE, L. SCOTT, AND M. POWELL. 1977a. The effects of experimental elevation of lake pH on the chemistry and biology of Nelson Lake near Sudbury, Ontario. Ont. Minist. Environ. Tech. Rep. 27 p.

YAN, N. D., W. A. SCHEIDER, AND P. J. DILLON. 1977b. Chemical and biological changes in Nelson Lake, Ontario, following experimental elevation of lake pH. Proc. Water Pollut. Res. 12: 213–231.

Amphibian Distribution with Respect to Pond Water Chemistry near Sudbury, Ontario

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Amphibians were present in 118 potential breeding sites 9–66 km northeast and southwest of Sudbury, Ontario. Detailed chemical analyses were done for 38 ponds, and 23 variables were subjected to principal components analysis to summarize the main gradients in pond chemistry. Discriminant analysis using scores of the first three principal components showed that the presence of *Rana pipiens, R. clamitans* and *Hyla crucifer* was positively related to buffering status (alkalinity, pH, and other correlated variables); the presence of *H. crucifer* was also negatively related to atmospheric deposition status (cadmium, nickel, other correlated metals, and sulphate). Discriminant analysis using the original water chemistry variables confirms these general patterns. Two species show relationships with buffering status variables: *Rana sylvatica* with conductivity and *R. clamitans* with alkalinity. Three species also show negative correlation with metal levels in pond water: *Bufo americanus* with nickel, *R. clamitans* with aluminum, and *R. pipiens* with zinc. Although most of the species expected do occur in the Sudbury area, the distributions of several species appear related to buffering status and metals present in their immediate environemnt. There were only two observations of *Ambystoma maculatum*, and low numbers of egg masses were noted for *R. sylvatica*.

Des amphibiens étaient présents dans 118 sites de reproduction potentiels entre 9 et 66 km au nord-est et au sud-ouest de Sudbury (Ontario). Nous avons effectué des analyses chimiques détaillées de 38 étangs et 23 variables ont été soumises à une analyse des principaux éléments afin de résumer les principaux gradients dans la chimie des étangs. L'analyse discriminante utilisant les points obtenus pour les trois premiers principaux éléments a montré une corrélation positive entre la présence de *Rana pipiens, R. clamitans* et *Hyla crucifer* et le pouvoir tampon (alcalinité, pH et autres variables corrélées); par ailleurs, on a observé une corrélation négative entre la présence de *H. crucifer* et la situation sur le plan des dépôts atmosphériques (cadmium, nickel, autres métaux corrélés et sulfate). L'analyse discriminante utilisant les variables hydrochimiques d'origine confirme ces tendances générales. La présence de deux espèces semble être reliée aux variables du pouvoir tampon : *Rana sylvatica* avec la conductivité et *R. clamitans* avec l'alcalinité. La présence de trois espèces montre par ailleurs une corrélation négative avec les concentrations de métaux dans l'eau des étangs : *Bufo americanus* avec le nickel, *R. clamitans* avec l'aluminium et *P. pipiens* avec le zinc. Même si la plupart des espèces prévues se retrouvent dans la région de Sudbury, la distribution de plusieurs espèces semble être reliée à capacité tampon et aux métaux présents dans leur environnement immédiat. On n'a observé qu'à deux reprises *Ambystoma maculatum* et on a noté que les nombres d'oeufs étaient faibles dans le cas de *R. sylvatica*.

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Many species of amphibians are potentially vulnerable to adverse impacts from acidic precipitation and atmospheric deposition of other contaminants including metals. About half of all frog species and one third of the salamander species breed in small ephemeral pools that fill up with rain and melted snow in early spring (Pough and Wilson 1977). The pH of the pools may be strongly influenced by the pH of precipitation and therefore may be lower than the pH of nearby ponds and lakes. Acidity is most pronounced during spring, and pH of these ponds is often low enough to cause mortality of amphibian embryos and tadpoles and alter population dynamics (Pough 1976; Beebee and Griffin 1977; Pough and Wilson 1977; Dunson and Connell 1982; Pierce et al. 1984; Dale et al. 1985a; Freda and Dunson 1986; Gascon and Planas 1986; Freda et al. 1991).

Although many amphibian species can breed in waters of low pH, other species, such as the spotted salamander (*Ambystoma maculatum*) and the leopard frog (*Rana pipiens*), may be more

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TABLE 1. Lethal[a] and critical[b] pH for embryos of eight of the amphibian species found in the Sudbury area.

Species	Lethal pH	Critical pH	Sources
Hyla crucifer	3.8–4.2	4.2	Dale et al. 1985a Karns 1983a Gosner and Black 1957
Hyla versicolor	3.8	4.3	Gosner and Black 1957
Rana sylvatica	3.5–4.0	3.9–4.25	Freda and Dunson 1986 Gascon and Planas 1986 Clark and LaZerte 1985 Dale et al. 1985a Pierce et al. 1984 Karns 1983a Gosner and Black 1957
Rana pipiens	4.2–4.5	4.6	Freda and McDonald 1990 Freda et al. 1990 Freda and Dunson 1985 Karns 1983a
Rana clamitans	3.7–3.8	4.1	Freda and Dunson 1986 Gosner and Black 1957
Rana catesbeiana	3.9	4.3	Saber and Dunson 1978 Gosner and Black 1957
Bufo americanus	3.8–4.2	4.0–4.2	Freda and McDonald 1990 Clark and LaZerte 1987 Clark and LaZerte 1985 Dale et al. 1985a Freda and Dunson 1985 Karns 1983a
Ambystoma maculatum	4.0–4.5	4.5–5.0	Clark and LaZerte 1987 Dale et al. 1985a Freda and Dunson 1985 Pough and Wilson 1977

[a]The pH that kills 85% or more of the embryos within a few hours (Gosner and Black 1957).
[b]The pH that causes high embryonic mortality, with effects that are more complex and less direct than lethal effects (Gosner and Black 1957).

sensitive (Table 1). Habitat acidity has been linked to reduced population size and shrinking geographical range of amphibians (Gosner and Black 1957; Cooke and Frazer 1976; Beebee and Griffin 1977; Saber and Dunson 1978). Baker et al. (1991) have reviewed the toxicological and ecological effects of acidic water on amphibians.

The concentration of metals in lakes which are influenced both by direct atmospheric deposition and by mobilization from substrates through the acidification process (Kelso et al. 1982) may also affect amphibians (Freda 1991). Copper, zinc, and iron are all toxic to amphibians (Lande and Guttman 1973; Porter and Hakanson 1976). We could also infer from studies of fish (Spry et al. 1981) that metals such as nickel, lead, cadmium, and manganese might have deleterious effects on amphibian populations.

The objective of this study was to determine whether amphibians in the highly stressed Sudbury, Ontario, area are being affected by adverse chemical conditions. Two smelting operations near the city together represent the greatest point source of sulphur emissions in the world. An atmospheric deposition gradient exists among lakes, as evidenced by elevated levels of sulphate, copper, nickel, zinc, lead, and iron (Pitblado et al. 1980). Many lakes in the Sudbury area have had pH reductions of more than 2 pH units during recent decades (Beamish and Harvey 1972; Ontario Ministry of the Environment 1982). Anthropogenic rather than geological sources have also been shown for sulphate anions in ponds and wetlands adjacent to Sudbury (Glooschenko and Stevens 1986).

Methods

Study Sites

Effects of pollutants from the smelting operations near Sudbury are more pronounced in the northeast–southwest direction due to the prevailing winds (Ontario Ministry of the Environment 1982) as well as the presence of lakes in sensitive bedrock in that area (Keller et al. 1992). In 1982 and 1983, 118 potential amphibian breeding sites (roadside ditches, ephemeral woodland ponds, and gravel pits) were surveyed at distances from Sudbury ranging from 9 to 66 km. At 38 of these sites (Fig. 1, precise locations available from authors) the surface water chemistry of the ponds was determined. We chose sites that were located either northeast or southwest of Sudbury and accessible by road. The ponds varied in size from 20 to 7500 m^2.

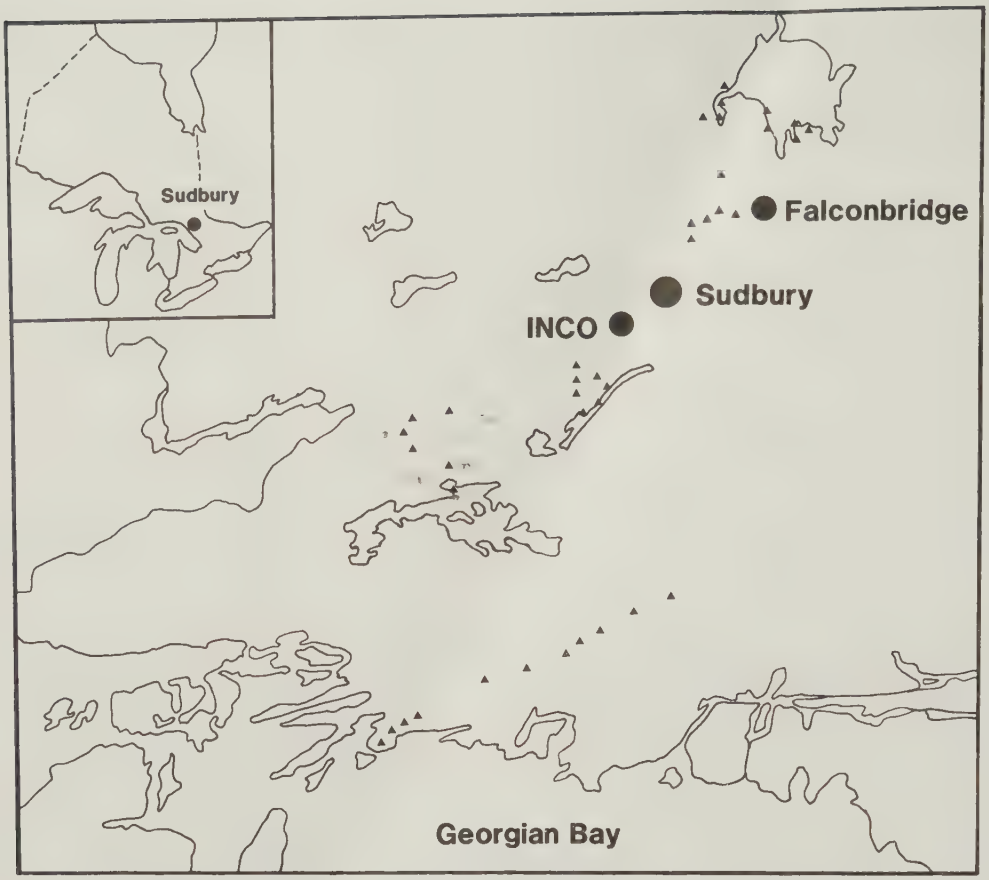

FIG. 1. Sampling sites for amphibian distribution and pond water chemistry in the vicinity of Sudbury, Ontario.

Data Collection

Between 4 May and 27 May 1982, 73 sites were surveyed for amphibian presence. This constituted the main portion of a broad survey of amphibian distribution in the Sudbury region. From 5 May to 10 May 1983, an additional 45 sites were surveyed; at 38 of these sites, surface water samples were taken between 4 May and 27 May 1982. In both years, investigations began following a period when both day and night air temperatures remained above freezing for about 1 wk. Because of the observed temperatures and precipitation levels, movements of spring-breeding amphibians would have begun by these dates. It was too early in the year for observation and quantification of larvae and embyros.

Species presence was established by visual or auditory means. The ponds were shallow enough that they could be traversed by an observer wearing chest waders. Systematic searches using a dip net were made for adults, juveniles, and egg masses and numbers of singing males were counted.

Surface water samples were taken at the time that amphibian observations were made. Pond water pH was measured in the field using a Canlab portable digital pH meter (model H5503-1). Water samples were stored on ice at about 4°C and forwarded immediately to the Ontario Ministry of the Environment in Rexdale for chemical analyses.

Laboratory analyses for conductivity, pH, and alkalinity were conducted using potentiometry. Laboratory pH rather than field pH determinations were used in all data analyses. True colour, chloride, fluoride, total organic carbon, nitrite and nitrate, ammonia, and silicate were assessed by colorimetry. Atomic absorption spectrophotometry formed the basis of assessing iron, manganese, calcium, magnesium, sodium, and potassium. Inductively coupled plasma atomic emission spectrometry was used to determine levels of aluminum, cadmium, copper, lead, nickel, and zinc.

Water samples taken in 1983 were analyzed for total aluminum, but not inorganic monomeric aluminum which may have an increased effect at low pH (Clark and Hall 1985; Clark and LaZerte 1985; Freda and Dunson 1986; Freda et al. 1990). In 1984, we returned to the area and collected water samples for analysis of inorganic monomeric aluminum as well as the other water chemistry variables from the 38 sites.

Data Analysis

Multivariate analysis was employed to examine relationships between the occurrence of the six anuran species and the water chemistry variables. The latter variables are all interrelated and collectively represent a number of underlying ecological gradients as well as human-induced stress gradients. To examine these multivariate gradients, we used both principal components and discriminant analyses.

For each of the amphibian species, the scores of the first three principal components were entered into a backward elimination discriminant function to determine the principal components that had a statistically significant ($P < 0.05$) effect on the presence of the species (Dillon and Goldstein 1984). These significance tests must, however, be regarded as approximate because principal component scores are not completely independent (Carter 1980).

A discriminant analysis was also used to identify the original water chemistry variables which had a statistically significant

TABLE 2. Quartimax rotated factor matrix and ranges for 23 chemical variables in 38 ponds (for each variable, an asterisk appears beside the highest component loading). All variables except pH were log-transformed for the principal components analysis.

Variable	Range	Principal component loadings 1	2	3
pH	4.3–7.3	0.66*	−0.32	0.38
Alkalinity (mg/L)	−3.1–40	0.73*	−0.31	0.26
Conductivity (μmho/cm)	20–1160	0.86*	0.21	0.08
DOC (mg/L)	1.6–35	0.36	−0.02	0.76*
Colour (Hazen)	3.8–305	0.22	−0.07	0.84*
Aluminum (total) (μg/L)	75–1300	−0.07	0.59*	0.41
Sulphate (mg/L)	4.8–303	0.58*	0.53	−0.23
Copper (μg/L)	1–68	0.31	0.74*	0.19
Nickel (μg/L)	1–670	0.13	0.85*	−0.31
Cadmium (μg/L)	0.2–1.0	0.32	0.74*	−0.30
Manganese (μg/L)	5.5–380	0.00	0.60*	−0.16
Zinc (μg/L)	3–139	−0.09	0.74*	0.08
Iron (μg/L)	35–6450	0.40	0.10	0.75*
Lead (μg/L)	3–11	0.63*	0.23	0.06
Silicates (μg/L)	20–5180	0.05	0.42*	0.13
Fluoride (μg/L)	22–250	0.38*	0.19	−0.27
Ammonia (μg/L)	1–820	0.61*	−0.04	−0.15
Calcium (μg/L)	1.1–105	0.89*	0.29	0.09
Magnesium (μg/L)	0.38–18.0	0.88*	0.17	0.27
Potassium (mg/L)	0.2–9.7	0.88*	0.09	0.12
Sodium (mg/L)	0.6–180	0.76*	−0.18	0.14
Chloride (mg/L)	0.1–332	0.72*	−0.23	0.12
Nitrate (mg/L)	2–1950	0.76*	0.23	0.06

effect on species occurrences. In this case, the discriminant functions differentiate sites occupied by a species from those unoccupied.

The small sample size ($n = 38$) relative to the number of variables (23) increases the chance of the analysis showing statistically significant relationships when in fact there are none (Williams 1983; Dillon and Goldstein 1984). Consequently, a number of checks on inferences were implemented. Separate stepwise discriminant analyses (using backward elimination) were performed using the water chemistry data collected in 1982–83 and data from 1984. We surmised that those variables important in both sets of data would probably reflect real patterns. The directions of the effects were also checked for consistency and for ecological meaning.

The smaller sets of variables derived by the principal components analysis were then subjected to a standard discriminant analysis to better estimate the canonical variates and misclassification rates. The nonparametric Epanechnikov kernel method of deriving the discriminant functions was used (Hand 1982). The Mahalanobis distance, based on the within-group covariance matrices, was the distance measure used (Dillon and Goldstein 1984).

All variables except pH were log-transformed to minimize departures from the multivariate normal distribution and heterogeneity of the variance–covariance matrices, both assumptions of parametric discriminant analysis (Lachenbruch 1975; Williams 1981, 1983; Dillon and Goldstein 1984). Nevertheless, in some cases, departures from these assumptions did occur. In the simple discriminant analyses, the nonparametric

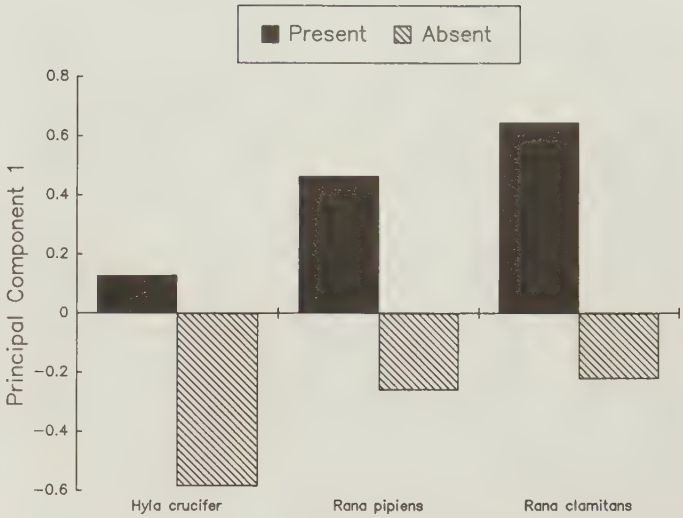

FIG. 2. Average principal component 1 scores for ponds where *H. crucifer, R. pipiens* and *R. clamitans* were present compared with ponds where the species were absent. Significance levels in discriminant analyses: $p < 0.05$ for *H. crucifer*, $p < 0.01$ for *R. pipiens*, and $p < 0.001$ for *R. clamitans*.

kernel method was used, based on the separate within-group covariance matrices. Pooled covariance matrices are required for backward elimination discriminant analyses and the technique is used here to identify important variables, not to make statistical inferences.

However, it is generally accepted that ecological data will often violate some assumptions of discriminant analysis (Williams 1981, 1983). Because discriminant analysis may be robust with respect to moderate departure from these assumptions, it is still regarded as a reasonable method for exploring relationships in multivariate ecological data (Williams 1981, 1983).

Results

Species Occurences

Of the 13 amphibian species that could occur in the Sudbury area and breed in ponds (Cook 1984), 12 were found among the 118 sites examined. Evidence of breeding (calling and/or egg masses) was found for five of these: *Hyla crucifer, Rana sylvatica, R. pipiens, Bufo americanus*, and *A. maculatum*. No evidence of breeding was found for *Hyla versicolor, Ambystoma laterale, Rana clamitans, R. septentrionalis*, and *R. catesbeiana*. The latter three species are late breeders and usually breed in more permanent waters. Sufficient data were available to relate the presence of six of the species to the 23 variables we measured. The two most common species found were *H. crucifer* and *R. sylvatica* which were each found in 32 ponds. *Rana pipiens* was found in 14 sites, *B. americanus* in 13, *R. clamitans* in 10, and *H. versicolor* in nine. The other six species were found in six or fewer ponds (*Plethodon cinereus, R. septentrionalis, R. catesbeiana, A. maculatum, A. jeffersonianum* complex, and *A. laterale*).

Principal Components Analysis

The first principal component, extracted from the 1982–83 pond chemistry data (38 sites), loaded highly (>0.60) and positively on pH, alkalinity, conductivity, calcium, magnesium, potassium, sodium, chloride, nitrate, ammonia, and lead and less highly (<0.60) on iron and sulphate (Table 2); we named

it "buffering status" as per Pitblado et al. (1980). We named the second principal component "atmospheric deposition status" because it loaded highly on nickel, copper, zinc, manganese, and cadmium and less highly on sulphate and aluminum. The third principal component (organic/mineral status) loaded highly on dissolved organic carbon (DOC), colour and iron and less highly on total aluminum. Collectively, these three principal components explain 63% of the variance in the correlation matrix. A principal components analysis on the 1984 water chemistry data showed similar results and so is not presented here. Ponds with high buffering status scores were more likely to have *H. crucifer, R. pipiens*, and *R. clamitans* than ponds with low scores (Fig. 2; $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively). In addition, ponds with high atmospheric deposition status scores (principal component 2) were less likely to have *H. crucifer* than ponds with low scores.

Discriminant Analysis

Discriminant analysis of the original water chemistry variables for each of the six species indicated that a number of variables contributed significantly to discrimination between ponds in which amphibians were present and those in which they were absent. Two species showed relationships with buffering status variables. *Rana sylvatica* was negatively related to conductivity ($p < 0.0001$ in the 1982–83 data and $p < 0.001$ in the 1984 data). *Rana clamitans* was positively related to alkalinity ($p < 0.05$ in the 1982–83 data and $p < 0.01$ in the 1984 data).

The concentrations of certain metals in pond water were also negatively related to the occurrence of three species: *B. americanus* with nickel ($p < 0.001$ in the 1982–83 data and $p < 0.05$ in the 1984 data), *R. pipiens* with zinc ($p < 0.05$ in both the 1982–83 and 1984 data), and *R. clamitans* with aluminum. For the latter species, total aluminum, the only measure of aluminum concentration taken in 1982–83 was significant in differentiating occupied and unoccupied habitat ($p < 0.0001$ in the 1982–83 data). In the 1984 data, inorganic monomeric aluminum was the significant variable in discriminating sites where *R. clamitans* ws present from those where it was absent ($p < 0.01$). Concentrations of nickel, aluminum, and zinc in the 38 ponds were, in some cases, extremely high relative to levels recorded in other studies (Table 3; Kelso et al. 1982; Freda et al. 1990).

Inorganic monomeric aluminum levels varied from 1 to 834 μg/L in the 38 ponds surveyed in 1984. Above pH 5.4, monomeric aluminum levels were always less than 114 μg/L. Below pH 5.0, monomeric aluminum levels varied widely, from 193 to 834 μg/L. Overall, inorganic monomeric aluminum was linearly related to pH when log-transformed (Fig. 3).

Metal concentrations were generally much higher in the ponds that we sampled than in ponds located somewhat farther away from Sudbury (40–66 km) (Table 3). Numbers of ponds within each pH range and associated DOC (milligrams per litre) are shown in Table 4.

A few other variables were significant in discriminant analyses performed on both the 1982–83 and 1984 data. Chloride concentration was positively correlated with *H. crucifer* presence ($p < 0.0001$ in the 1982–83 data and $p < 0.05$ in the 1984 data), and fluorine was also positively related to *B. americanus* ($p < 0.05$ in both the 1982–83 and 1984 data) and *R. clamitans*. No variables were significant in differentiating those sites occupied and unoccupied by *H. versicolor.*

Discussion

Buffering Status of Pond Habitat

We found significant relationships between buffering status and the presence of *H. crucifer, R. pipiens,* and *R. clamitans*. Because buffering status decreases as water becomes acidic, acidification of amphibian breeding ponds may cause the loss of some species, although our data do not allow us to determine the mechanism by which this occurs. Other habitat characteristics that we did not measure but that are important in determining amphibian presence could be correlated with buffering status or atmospheric deposition status. For example, pond size, pond depth, percent cover of the surrounding vegetation, and the amount of emergent vegetation are important for most amphibian species.

As in the present study, Clark and Euler (1982) also found low densities of *H. crucifer* near low-pH waters. Other workers have reported reduced hatching success of *R. pipiens* eggs in bog water of pH 4.2 and 4.4 (Karns 1983b; Freda et al. 1990). We found *A. maculatum* in only two of the 118 ponds that we surveyed, although the Sudbury area is well within the range of this species. *Ambystoma maculatum* is highly sensitive to acidification (Table 1). In a survey done in central Ontario (Clark 1986), it was noted that the number of *A. maculatum* egg masses per pond was positively correlated with alkalinity and pond area, while percent hatching success was correlated with pond pH and calcium concentration.

Both the maximum number of *R. sylvatica* egg masses per pond (39) and the maximum number of egg masses per communal aggregate (36) that we found were much lower than the numbers found by other researchers. Several studies have reported communal aggregates which often contained eggs from more than 100 females (Wells 1977; Howard 1980). Seale

TABLE 3. Metal levels in pond waters in areas of varying distance from Sudbury. All units are in μg/L.

Metal	This study, 9–66 km from Sudbury	Wanapitei Lake area (Blancher and McNicol 1986), 40–66 km from Sudbury	Ranger Lake area (Blancher and McNicol 1986), 200 km from Sudbury
Iron	35–6450	52–460	30–160
Cadmium	0.2–1.0	<1.0	<1.0
Manganese	5.5–380	4.5–92.5	5.7–41.7
Copper	1–68	<1.0–7.3	0–<1.0
Nickel	1–670	3.3–19.5	0–1.0
Lead	3–11	0–2.7	<1.0–1.9
Zinc	3–139	2.2–15.9	2.7–12.9
Aluminum	75–1300	31–228	43–213

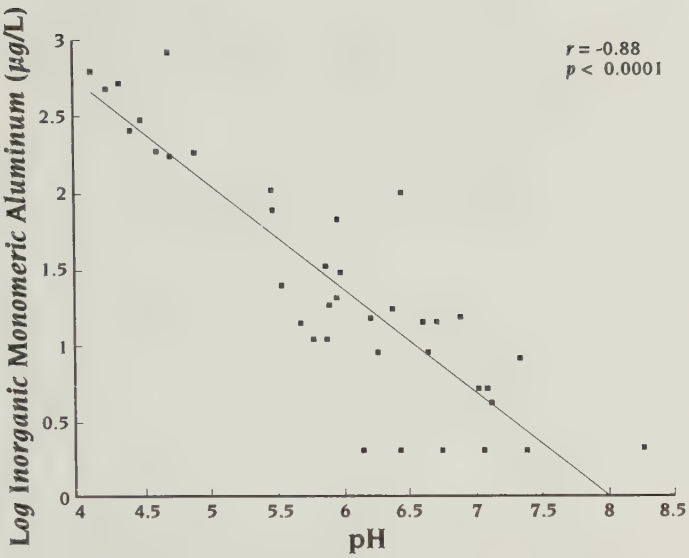

FIG. 3. Relationship between inorganic monomeric aluminum and pH.

TABLE 4. DOC in Sudbury area ponds within several pH ranges (there were no ponds located in the 5.0–5.5 pH range).

DOC (mg/L)	No. of ponds	pH range
<5.7	7	4.0–5.0
	16	5.5–7.5
>5.7	2	<4.8
	13	5.5–7.5

(1982) found that in ponds in Pennsylvania of a size range comparable with ours, the maximum number of egg masses per pond was greater than 1000, and the largest communal oviposition site contained 963 egg masses. One pond in New York State that was about 1500 m^2 had 686 egg masses, all deposited at one communal site (Waldman 1982). Reduced numbers of *R. sylvatica* egg masses in the Sudbury ponds may be attributed to inhibitory effects of low pH. Gascon and Planas (1986) reported that acidity (pH 3.4–5.5) and total organic carbon (15.6 mg/L) were negatively correlated with the density of *R. sylvatica* egg masses in breeding ponds in Quebec. Hatching success was reduced and mould increased in low-pH ponds.

Influence of Metal Concentrations

The metal levels in the ponds that we surveyed were generally much higher than levels found in ponds located further away from Sudbury (Table 3) and in other studies (Freda et al. 1990). In the case of five metals that we measured, levels in at least some of the ponds exceeded levels given in the literature as having harmful effects on amphibians, or on fish when metal toxicity data on amphibians were not available (Brown 1968; Lewis 1978; Spry et al. 1981).

Copper concentrations of 60 µg/L inhibited growth of *R. pipiens* larvae, while newly hatched larvae had a 72-h LC50 of 150 µg/L (Lande and Guttman 1973). Lethal concentrations of copper, zinc, and iron for permetamorphic toads (*Bufo boreas*) were 20–44 µg/L, 100–500 µg/L, and 20–30 mg/L, respectively (Porter and Hakanson 1976). Embryos of *Rana temporaria* were not affected by exposure of up to 4 µg Cd/L at pH 4.0, 4.5 and 6.0, although this same level was toxic to larvae (Leuven et al. 1986). In eastern Virginia, Blem and Blem (1991) noted that high aluminum, copper, silicon, and zinc concentrations in breeding ponds were associated significantly with decline in reproductive activity and in density of *A. maculatum*. Considerably more information on metal toxicity exists for fish. Metal concentrations in softwater Ontario lakes that had adverse effects on fish were 380–730 µg Ni/L, 0.7 µg Cd/L, 4–8 µg Pb/L, and 770–1530 µg Mn/L (Spry et al. 1981). We encountered similar levels of all these metals except manganese in some of our ponds (Table 3). Metal levels and low pH may therefore be a limiting factor for successful breeding of *A. maculatum* and possibly for other amphibian species in the Sudbury ponds we surveyed.

At pH 4.3, 46 µg inorganic monomeric Al/L was more toxic to *B. americanus* and *R. sylvatica* than 34 µg inorganic monomeric Al/L (Clark and Hall 1985). Levels as low as 10–20 µg/L can also decrease hatching success at pH 4.1–4.3 (Clark and LaZerte 1985). In 23% of Sudbury ponds, we observed six with inorganic monomeric aluminum above 250 µg/L and three others at or slightly below 200 µg/L (Fig. 3).

Freda and McDonald (1990) have reported that aluminum can ameliorate the toxic effects of very low pH (4.2–4.4) for embryos of *R. pipiens* but that at higher pH's (4.6–4.8), aluminum is toxic. This was also reported for *A. maculatum* (Clark and LaZerte 1987). For other species such as *B. americanus*, *H. crucifer*, and *R. temporaria*, aluminum toxicity increases with decreasing pH (Dale et al. 1985b; Clark and LaZerte 1987; Andren et al. 1988). Some amelioration of the toxic effect of aluminum may have occurred therefore in approximately 8.0% of the lower pH Sudbury ponds. However, the labile aluminum found toxic to these species may also have been found in approximately 8.0% of those Sudbury ponds at slightly higher pH (4.6–4.8). Albers and Prouty (1987) reported that embryonic survival of *A. maculatum* was negatively correlated with concentration of aluminum in temporary ponds in Maryland. The range of total aluminum (0.08–1.38 ppm) found by these authors is similar to that we have reported for the Sudbury ponds.

It is known that humic substances in natural water can bind aluminum (Pott et al. 1985; Backes and Tipping 1987). Monomeric aluminum toxicity may also have been ameliorated by complexation with organic ligands, as has been found in fish (Driscoll et al. 1980; Neville 1985; Hutchinson and Sprague 1987). In a study to determine the effect of a range of total aluminum (250–1000 µg/L) on *R. pipiens* embryos at pH 4.8, Freda et al. (1990) reported that DOC exceeding 5.7 mg/L complexed most of the aluminum present, decreasing labile aluminum. Although below pH 4.8, two of our ponds had DOC levels above 5.7 mg/L which may have decreased potentially toxic labile aluminum. In contrast, seven of the survey ponds (17.9%) between pH 4.0 and 5.0 had DOC levels below 4.00 mg/L, and therefore, aluminum toxicity may not have been ameliorated under these conditions for *A. maculatum* and *R. pipiens* early life stages (Table 4).

DOC itself can be toxic to amphibian embryos (Karns 1983a; Freda and Dunson 1986). This is inversely related to pH. Dilutions of bog water containing DOC from 5.7 to 15.6 mg/L increased mortality of *R. pipiens* embryos at pH 4.2 but had no toxic effects at pH 4.8 (Freda et al. 1990). In addition, humic compounds in dark waters act as a sink for toxic metals which may contribute to water toxicity (Reuter and Perdue 1977). This may have occurred in some of the Ontario ponds with high metal concentration.

Generalizing from the foregoing information, we might deduce that amphibians may have been limited by nickel, alu-

minum, zinc, copper, or DOC in some of our ponds (Tables 2, 3, 4). Our study did find a negative relationship between *R. clamitans* and inorganic monomeric aluminum (1984) or total aluminum (1982–83). In addition, the absence of *B. americanus* and *R. pipiens* was associated with high nickel and zinc levels, respectively. The absence of *H. crucifer* was associated with both low buffering stuatus and high metal loading. The small number of egg masses of *R. sylvatica* and the absence of *A. maculatum* from nearly all of the sites are also noteworthy.

In conclusion, the distributions of *R. pipiens, H. crucifer,* and *R. clamitans* appear to be adversely affected by changes in buffering status associated with acidification in ponds near Sudbury, Ontario. In addition, the presence of *B. americanus, R. clamitans, H. crucifer,* and possibly *R. pipiens* appears to be negatively related to high concentrations of metals often associated with aerial deposition; these may have lethal effects on amphibian embryos and larvae. The absence of three of the species from low-pH ponds in our study may therefore have resulted from combined effects and interactions of low pH and DOC and high monomeric aluminum and other metals.

This preliminary survey of amphibian distribution undertaken in 1983–84 indicates that conditions unfavourable to successful amphibian reproduction existed in ponds near Sudbury at that time. With reports of widespread amphibian decline throughout North America and elsewhere, this study may provide background data for regional monitoring programs to assess current amphibian distribution and habitat suitability and document future amphibian population trends.

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References

Albers, P. H., and R. M. Prouty. 1987. Survival of spotted salamander eggs in temporary woodland ponds of coastal Maryland. Environ. Pollut. 46: 45–61.

Andren, C., L. Henrikson, M. Olsson, and G. Nilson. 1988. Effects of pH and aluminum on embryonic and early larval stages of Swedish brown frogs *Rana arvalis, R. temporaria* and *R. dalmatina*. Holarct. Ecol. 11: 127–135.

Backes, C. A., and E. Tipping. 1987. Aluminum complexation by an aquatic humic fraction under acidic conditions. Water Res. 21: 211–216.

Baker, J. P., D. P. Bernard, S. W. Christensen, M. J. Sale, J. Freda, K. Heltcher, L. Rowe, P. Scanlon, P. Stokes, G. Suter, and W. Warren-Hicks. 1991. Biological effects of changes in surface water acid–base chemistry. State-of-Science/Technology Report 13. National Acid Precipitation Assessment Program. Washington, DC.

Beamish, R. J., and H. H. Harvey. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board. Can. 29: 1131–1143.

Beebee, T. J. C., and J. R. Griffin. 1977. A preliminary investigation into natterjack toad (*Bufo calamita*) breeding site characteristics in Great Britain. J. Zool. 181: 341–350.

Blancher, P. J., and D. K. McNicol. 1986. Investigations into the effects of acid precipitation on wetland-dwelling wildlife in northeastern Ontario. Technical Report Series No. 2. Ontario Region, Canadian Wildlife Service. 153 p.

Blem, C. R., and L. B. Blem. 1991. Cation concentrations and acidity in breeding ponds of the spotted salamander *Ambystoma maculatum* (Shaw) in Virginia. Brimleyana 17: 67–76.

Brown, V. M. 1968. The calculation of the acute toxicity of mixtures of poisons to the rainbow trout. Water Res. 2: 723–733.

Carter, E. 1980. Tests of location based on principal components, p. 47–52. *In* R. Gupta [ed.] Multivariate statistical analysis. North-Holland Publishing Company, Amsterdam, The Netherlands.

Clark, K. L. 1986. Responses of spotted salamander, *Ambystoma maculatum*, populations in central Ontario to habitat acidity. Can. Field-Nat. 100: 463–469.

Clark, K., and D. Euler. 1982. The importance of pH and habitat disturbance in amphibian distribution in central Ontario. Ontario Ministry of Natural Resources, Whitney Black, Queen's Park, Toronto, Ont.

Clark, K. L., and R. J. Hall. 1985. Effects of elevated hydrogen ion and aluminum concentrations in the survival of amphibian embryos and larvae. Can. J. Zool. 63: 116–123.

Clark, K. L., and B. D. LaZerte. 1985. A laboratory study of the effects of aluminum and pH on amphibian eggs and tadpoles. Can. J. Fish. Aquat. Sci. 42: 1544–1551.

1987. Intraspecific variation in hydrogen on and aluminum toxicity in *Bufo americanus* and *Ambystoma maculatum*. Can. J. Fish. Aquat. Sci. 44: 1622–1628.

Cook, F. R. 1984. Introduction to Canadian amphibians and reptiles. National Museums of Canada, Ottawa, Ont. 200 p.

Cooke, A. S., and J. F. D. Frazer. 1976. Characterization of newt breeding sites. J. Zool. 178: 223–236.

Dale, J. M., B. Freedman, and J. Kerekes. 1985a. Acidity and associated water chemistry of habitats in Nova Scotia. Can. J. Zool. 63: 97–105.

1985b. Experimental studies of the effects of acidity and associated water chemistry on amphibians. Proc. N.S. Inst. Sci. 35: 35–54.

Dillon, W., and M. Goldstein. 1984. Multivariate analysis. Methods and applications. Wiley, New York, NY. 587 p.

Driscoll, C. T., J. P. Baker, J. J. Bisogni, and C. L. Schofield. 1980. Effect of aluminum speciation on fish in dilute acidified waters. Nature (Lond.) 284: 161–164.

Dunson, W. A., and J. Connell. 1982. Specific inhibition of hatching in amphibian embryos by low pH. J. Herpetol. 16: 314–316.

Freda, J. 1991. The effects of aluminum and other metals on amphibians. Environ. Pollut. 71: 305–328.

Freda, J., V. Cavdek, and D. G. McDonald. 1990. The role of organic complexation in the toxicity of metals to amphibians. Can. J. Fish. Aquat. Sci. 47: 217–224.

Freda, J., and W. A. Dunson. 1985. Field and laboratory studies of ion balance and growth rates of ranid tadpoles chronically exposed to low pH. Copeia 1985: 415–423.

1986. Effects of low pH and other chemical variables on the local distribution of amphibians. Copeia 1986: 454–466.

Freda, J., and D. G. McDonald. 1990. Effects of aluminum on the leopard frog, *Rana pipiens*: life stage comparisons and aluminum uptake. Can. J. Fish. Aquat. Sci. 47: 210–216.

Freda, J., W. J. Sadinski, and W. A. Dunson. 1991. Long term monitoring of amphibian populations with respect to the effects of acidic deposition. Water Air Soil Pollut. 55: 445–462.

Gascon, C., and D. Planas. 1986. Spring pond water chemistry and the reproduction of the wood frog, *Rana sylvatica*. Can. J. Zool. 64: 543–550.

Glooschenko, V., and W. Stevens. 1986. Sources of acidity in wetlands near Sudbury, Ontario. Sci. Total Environ. 54: 53–59.

Gosner, K. L., and I. H. Black. 1957. The effects of acidity on the development and hatching of New Jersey frogs. Ecology 38: 256–262.

Hand, D. 1982. Kernel discriminant analysis. Research Studies Press, New York, NY.

Howard, R. D. 1980. Mating behavior and mating success in woodfrogs, *Rana sylvatica*. Anim. Behav. 28: 705–716.

Hutchinson, N. J., and J. B. Sprague. 1987. Reduced lethality of Al, Zn, and Cu mixtures to American flagfish by complexation with humic substances in acidified soft waters. Environ. Toxicol. Chem. 6: 1–11.

Karns, D. R. 1983a. Toxic bog water in northern Minnesota peatlands: ecological and evolutionary consequences for breeding amphibians. Ph.D. dissertation, University of Minnesota, Minneapolis, MN.

1983b. The role of low pH in the toxicity of bog H_2O to amphibian embryos. Bull. Ecol. Soc. Am. 64: 188.

Keller, W., J. R. Pitblado, and J. Carbone. 1992. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 25–32.

Kelso, J., R. Love, J. Lipsit, and R. Dermott. 1982. Chemical and biological status of headwater lakes in the Sault Ste. Marie District, Ontario, p. 165–

208. *In* F. D'Itri [ed.] Acid precipitation: effects on ecological systems. Ann Arbor Science Publishers, Ann Arbor, MI.

LACHENBRUCH, P. 1975. Discriminant analysis. Hafner Press, New York, NY. 128 p.

LANDE, S. P., AND S. I. GUTTMAN. 1973. The effects of copper sulphate on the growth and mortality of *Rana pipiens* tadpoles. Herpetologica 29: 22–27.

LEUVEN, R. S. E. W., C. DEN HARTOG, M. M. C. CHRISTIAANS, AND W. H. C. HEIJLIGERS. 1986. Effects of water acidification on the distribution pattern and reproductive success of amphibians. Experimentia 42: 495–503.

LEWIS, M. 1978. Acute toxicity of copper, zinc and manganese in single and mixed salt solutions to juvenile longfin dace, *Agosia chrysogaster*. J. Fish Biol. 13: 695–700.

NEVILLE, C. M. 1985. Physiological responses of juvenile rainbow trout, *Salmo gardineri*, to acid and aluminum — prediction of field responses from laboratory data. Can. J. Fish. Aquat. Sci. 42: 2004–2019.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1982. Sudbury environmental study. 40 St. Clair Ave. W, Toronto, Ont.

PIERCE, B. A., J. B. HOSKINS, AND E. EPSTEIN. 1984. Acid tolerance in Connecticut wood frogs (*Rana sylvatica*). J. Herpetol. 18: 159–167.

PITBLADO, J. R., W. KELLER, AND N. I. CONROY. 1980. A classification and description of some northeastern Ontario lakes influenced by acid precipitation. J. Great Lakes Res. 6: 247–257.

PORTER, K. R., AND D. E. HAKANSON. 1976. Toxicity of mine drainage to embryonic and larval boreal toads. Copeia 1976: 327–331.

POTT, D. B., J. J. ALBERTS, AND A. W. ELZERMAN. 1985. The influence of pH on the binding capacity and conditional stability constants of aluminum and naturally-occurring organic matter. Chem. Geol. 48: 293–304.

POUGH, F. H. 1976. Acid precipitation and embryonic mortality of spotted salamanders, *Ambystoma maculatum*. Science (Wash., DC) 192: 68–70.

POUGH, F. H., AND R. E. WILSON. 1977. Acid precipitation and reproductive success of *Ambystoma* salamanders. Water Air Soil Pollut. 7: 307–316.

REUTER, J. H., AND E. M. PERDUE. 1977. Importance of heavy metal – organic interactions in natural waters. Geochim. Cosmochim. Acta 41: 325–334.

SABER, P. A., AND W. A. DUNSON. 1978. Toxicity of bog water to embryonic and larval anuran amphibians. J. Exp. Zool. 204: 33–42.

SEALE, D. B. 1982. Physical factors influencing oviposition by the woodfrog, *Rana sylvatica*, in Pennsylvania. Copeia 1982: 627–635.

SPRY, D. J., C. M. WOOD, AND P. V. HODSON. 1981. The effects of environmental acid on freshwater fish with particular reference to the softwater lakes in Ontario and the modifying effects of heavy metals. A literature review. Can. Tech. Rep. Fish. Aquat. Sci. 999: 145 p.

WALDMAN, B. 1982. Adaptive significance of communal oviposition in wood frogs (*Rana sylvatica*). Behav. Ecol. Sociobiol. 10: 169–174.

WELLS, K. D. 1977. The social behaviour of anuran amphibians. Anim. Behav. 25: 666–693.

WILLIAMS, B. 1981. Discriminant analysis in wildlife research: theory and applications, p. 59–71. *In* D. Capen [ed.] The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. U.S. Department of Agriculture, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.

1983. Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283–1291.

Distribution of Waterfowl Broods in Sudbury Area Lakes in Relation to Fish, Macroinvertebrates, and Water Chemistry

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We studied habitat selection by insectivorous waterfowl in 65 small lakes near Sudbury, Ontario. Data on environmental variables (pH, alkalinity, conductivity, calcium, total phosphorus, dissolved organic carbon (DOC), and area), fish, and littoral macroinvertebrates indicated that the distribution of broods was influenced by differences in invertebrate prey assemblages in lakes with differing degrees of acid stress and types of fish predation. Lakes ranged in pH from 4.2 to 7.7 (mean = 5.8); 40% were fishless, 43% were dominated by yellow perch (*Perca flavescens*) or white sucker (*Catostomus commersoni*) (YP/WS), and the remainder contained only small cyprinids, sticklebacks, or darters (C/S). Fishless lakes were more acid than lakes with fish. Compared with fishless lakes, C/S lakes had higher levels of DOC and YP/WS lakes were larger. Macroinvertebrate composition was strongly related to fish composition and suggested increasing predation along a gradient: fishless < C/S < YP/WS. pH-related variables distinguished lakes with a taxonomically rich benthos from those with a taxonomically poorer fauna. Insectivorous waterfowl selected fishless lakes over lakes with fish and C/S over YP/WS lakes. Lakes with species-rich, acid-sensitive invertebrate assemblages were not selected over those typified by species-poor, acid-tolerant ones.

Nous avons étudié le choix d'habitats d'oiseaux aquatiques insectivores de 65 petits lacs situés dans les environs de Sudbury (Ontario). Les variables environnementales (pH, alcalinité, conductivité, calcium, phosphore total, carbone organique dissous (COD) et superficie), les poissons et les macroinvertébrés du littoral indiquaient que la répartition des couvées dépendait des différences entre les assemblages d'invertébrés proies dans des lacs qui différaient entre eux par l'importance du stress acide et le type de prédation par les poissons. Les lacs présentaient un pH dont la gamme se situait entre 4,2 et 7,7 (moyenne de 5,8); 40% des lacs étaient dépourvus de poissons, 43% étaient dominés par la perchaude (*Perca flavescens*) ou le meunier noir (*Catostomus commersoni*) (P/MN) et les autres n'abritant que de petits cyprinidés, des épinoches ou des dards (C/E). Les lacs sans poissons étaient plus acides que ceux en abritant. Comparativement aux lacs sans poissons, les lacs à C/E présentaient des teneurs plus élevées de COD et les lacs à P/MN étaient plus grands. La composition en macroinvertébrés présentait une forte corrélation avec la composition en poissons et portait à croire à une augmentation de la prédation selon le gradient : lacs sans poissons < C/E < P/MN. Les variables liées au pH permettaient de distinguer les lacs à benthos à taxonomie riche de ceux à faune de taxonomie peu diversifiée. Les oiseaux aquatiques insectivores préféraient, dans l'ordre, les lacs sans poissons aux lacs C/E et aux lacs P/MN. Les lacs à assemblages d'invertébrés riches en espèces et sensibles à l'acidité n'étaient pas préférés aux lacs à assemblages pauvres en espèces et tolérants à l'acidité.

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Evidence of deleterious effects of acid precipitation on freshwater fauna has been widely reported (see reviews by Dillon et al. 1984; Schindler 1988; Muniz 1991). Where lakes have been acidified, dramatic changes in freshwater communities have occurred and include losses of fish populations and acid-sensitive invertebrates (Schindler et al. 1989; Kelso et al. 1990). As those organisms are food for waterfowl and other aquatic birds, there is concern that as lakes acidify, changes in the composition, abundance, and nutritional value of prey might influence their choice of breeding habitat (DesGranges and Darveau 1985; McNicol et al. 1987a) or breeding success (Eriksson 1984; McAuley and Longcore 1988a).

The effect of decreasing pH on waterfowl will vary with the severity of acidification and the foraging habits of the species. Several species feed exclusively on aquatic invertebrates during the breeding season, a source of high-protein, mineral-rich prey for egg production and rapid growth of young. Common goldeneyes (*Bucephala clangula*) prefer acid lakes to nonacid lakes (DesGranges and Darveau 1985; McNicol et al. 1987a) because they are less likely to support populations of fish that are effective competitors for invertebrate prey (Eriksson 1979; Eadie and Keast 1982; DesGranges and Rodrigue 1986). The influence of fish predation on the composition of macroinvertebrate communities has been demonstrated between fishless habitats and those containing fish (Macan 1977; Thorp 1986). However, a more general result of acidification is an overall reduction in species richness (Ford 1989; Schindler et al. 1989; Minns et al. 1990), which may occur at pHs capable of supporting fish (Raddum and Fjellheim 1984; Mills and Schindler 1986). Then, insectivorous waterfowl must compete with acid-tolerant fish populations for invertebrate prey and may also experience reduced availability of dietary calcium due to the loss of certain acid-sensitive invertebrates, such as molluscs and crustaceans (Scheuhammer 1991). Moreover, lakes with different fish assemblages, containing species with different foraging tactics and gape size (Keast and Webb 1966), are expected to have different macroinvertebrate assemblages. We

hypothesized that lakes populated only with small cyprinid or stickleback species would contain different macroinvertebrates than those populated with larger predators, such as yellow perch (*Perca flavescens*) or white sucker (*Catostomus commersoni*).

In this paper, we examine habitat selection by insectivorous waterfowl in small, acid-stressed lakes near Sudbury, Ontario. We investigate whether the distribution of broods was related to the composition of littoral macroinvertebrates found in lakes with differing degrees of acid stress and types of fish predation.

Study Area

Sixty-five lakes were surveyed in the Wanapitei area northeast of Sudbury, Ontario (46°45′N, 80°45′W). Most are small (80% below 10 ha) and are located in the headwater portion of watersheds. Such lakes provide the principal breeding habitat for several species of waterfowl (McNicol et al. 1987a). Wanapitei lies within the zone of historically high deposition of SO_2 extending northeast of Sudbury (Jeffries 1984) but is beyond the zone of high metal contamination that originates from the sulphide ore smelters. The heterogeneous nature of bedrock and surficial deposits in the area result in a broad range of lake pHs (Jeffries et al. 1984). Fish and invertebrate populations vary along the pH gradient (McNicol et al. 1987a). Recent chemical and biological recovery of some Sudbury area lakes has been attributed to reduced inputs of SO_2 from local sources (Keller and Pitblado 1986; Gunn and Keller 1990; Keller et al. 1992).

Materials and Methods

All lakes were sampled between 1983 and 1987 for pH, conductivity (Cond) (microsiemens per centimetre), alkalinity (Alk) (microequivalents per litre), calcium (Ca) (milligrams per litre), dissolved organic carbon (DOC) (milligrams per litre), total phosphorus (TP) (micrograms per litre), and size (Area) (hectares). Surface water samples were collected from 57 of 65 lakes during fall turnover. Of those, 12 lakes were sampled only once, 13 lakes were sampled in two years, and 32 lakes were sampled in at least three years. The remaining eight lakes were sampled once in June 1983. For lakes sampled more than once, a single value (arithmetic average) has been used for each chemical variable. All samples were filtered using Whatman 41 filters. Carbon samples were subsequently filtered using 0.45-μm millipore filters. Most study lakes were dilute (low Cond) and oligotrophic (low TP), with pHs ranging from extremely acid to circumneutral (43% below 5.5) (Table 1).

Each lake was sampled for fish at least once between 1983 and 1989. Ten lakes were sampled more than once with the analyses based on the most recent sampling of any given lake. Sampling consisted of placing a wire minnow trap baited with dry dog food at each of five to six equidistant locations in the littoral zone of each lake for 24 h (see Bendell and McNicol 1987a). Fish were preserved in 75% ethyl alcohol, identified to species, and counted. Hybrids of northern redbelly dace (*Phoxinus eos*) and finescale dace (*Phoxinus neogaeus*) were combined (*Phoxinus* spp.) for analysis.

In northern lakes used by waterfowl, floating *Sphagnum* mats and soft bottoms make seining difficult, and low conductivity reduces the effectiveness of electroshocking (Tonn 1985; He and Lodge 1990). In such habitats, small nongame fish species predominate and are effectively sampled by minnow traps (Tonn and Magnuson 1982; Tonn and Paszkowski 1986), which were used to distinguish among cyprinid assemblages in shallow Algoma lakes (Bendell and McNicol 1987a).

Each lake was sampled for macroinvertebrates once between late June and mid-July in either 1988 (37 lakes) or 1989 (28 lakes). In each lake, two types of samples were collected: (1) epibenthic organisms from sediment removed from a strip 0.5 × 0.3 m × 2–3 cm deep, with a D-frame net, and seived through 1-mm^2 mesh screens and (2) sweep samples designed to collect free-swimming insects (nekton), consisting of 10 sweeps over the bow of a forward moving canoe; each sweep described an arc from the surface of the water to near the substrate and back with a D-frame net. Ten benthic samples and 10 sweep samples were collected from randomly selected sites in the littoral zone (<1 m deep).

Macroinvertebrates were preserved in 70% ethyl alcohol, sorted, and identified to genus or species. Rare or difficult to identify taxa were combined at higher levels. Chironomidae and zooplankton were not collected, as they are not important in the diets of insectivorous waterfowl in the area (McNicol et al. 1987b). For each lake and sample type, an average abundance of each taxon was calculated. In ordination analyses, taxa present in at least two lakes were scored as absent from a lake, uncommon (0.1–0.9 individuals per sample), common (1.0–9.9), or abundant (≥10).

Waterfowl surveys were conducted between 1983 and 1987. Lakes were surveyed for broods at least twice each year, first in June and again in July, by walking or canoeing the entire shoreline of lakes and scanning with binoculars. In the analysis, "brood-present" lakes are those on which a brood, defined as one or more juveniles with or without hen, was observed during a survey in at least one year, while "brood-absent" lakes are those on which broods were never seen.

Statistical Analyses

Because large fish species are expected to influence the availability of invertebrate prey for juvenile waterfowl differently than small, gape-limited species, we classified lakes among

TABLE 1. Mean, confidence limits (±95% CL), range, and median values of environmental parameters in study lakes (N = 65).

Parameter	Units	Mean[a]	±95% CL	Range	Median
pH		5.8	5.6–6.0	4.2–7.7	5.7
Alk.	$\mu eq \cdot L^{-1}$	10.2	5.7–18.2	0–1551.4	10.1
Cond.	$\mu S \cdot cm^{-1}$	38.4	35.3–41.8	22.6–189.5	35.3
Ca	$mg \cdot L^{-1}$	3.5	3.0–4.0	1.5–33.7	3.1
DOC[b]	$mg \cdot L^{-1}$	5.7	5.1–6.4	1.1–18.2	5.9
TP	$\mu g \cdot L^{-1}$	6.8	6.1–7.6	0.1–16.0	6.4
Area	ha	4.6	3.5–6.1	0.1–60.0	4.8

[a]Back-transformed from $\log_e$ values (except pH).
[b]N = 64.

three categories: (1) fishless lakes, (2) lakes containing only small cyprinids, brook stickleback (*Culaea inconstans*), or Iowa darter (*Etheostoma exile*) (C/S lakes), and (3) lakes containing yellow perch or white sucker (YP/WS lakes). These categories represent a hypothetical gradient of fish predation effects on invertebrates from none in fishless lakes, through moderate in C/S lakes, to large in YP/WS lakes.

Lakes were grouped according to the degree of similarity in their respective macroinvertebrate assemblages by using the FORTRAN procedures TWINSPAN (Two-Way Indicator Species Analysis) and DECORANA (Detrended Correspondence Analysis) (Hill 1979a, 1979b). TWINSPAN arranges lakes and species into hierarchical groups; lakes are grouped on similarities in invertebrate species occurrence and abundance, and species are grouped by the degree to which they cooccur in lakes. DECORANA derives axes, uncorrelated with one another, and assigns scores to each lake. Lakes with widely separated DECORANA scores have different invertebrate faunas whereas lakes with similar scores have similar faunas. Benthic and sweep-sample-derived assemblages were analyzed separately in relation to environmental variables.

Environmental measurements, except pH, were $\log_e$ transformed. Variables that were poorly correlated with one another ($|r| < 0.5$) (PROC CORR, SAS Institute Inc. 1988) were used in a series of stepwise discriminant analyses (PROC STEPDISC) to identify the subset of variables that discriminated most strongly (maximum R^2, $P < 0.10$) among groups of lakes as defined by either their fish category or macroinvertebrate assemblage. For analyses of macroinvertebrate-derived TWINSPAN groupings of lakes, the fish category variable was also included as an explanatory variable, notwithstanding the fact that it was strongly correlated with several environmental variables, most notably pH. It was included because of its unique effect on macroinvertebrates through predation. Values of the fish variable were ordered along the hypothetical gradient with fishless lakes assigned a value of 0, C/S = 1, and YP/WS = 2. Explanatory variables identified by STEPDISC were used in a further discriminant analysis (PROC DISCRIM) that tested for differences among groups. Canonical variables were derived to summarize between-class variation.

One-way ANOVAs were used to examine effects of fish category on macroinvertebrate assemblage characteristics as defined by DECORANA axis scores for each lake. For tests with significant results, unplanned comparisons were made using the Tukey–Kramer method. *G*-tests of independence or Fisher exact tests were used to examine relationships between waterfowl brood use of lakes and (1) fish categories and (2) TWINSPAN-derived macroinvertebrate assemblages. Fisher exact tests were used only when expected values were below 5.0. Where *G*-tests on 3 × 2 tables produced significant results, a multiple comparisons procedure was used to examine these relationships (Sokal and Rohlf 1981).

Results

Fish

Of the 65 lakes sampled, 26 were fishless. Fifteen species (including both *Phoxinus* spp.) were recorded in 39 lakes. Yellow perch, *Phoxinus*, white sucker, and brook stickleback were common (Table 2). Other frequent species were fathead minnow (*Pimephales promelas*), Iowa darter, and pearl dace (*Magariscus margarita*). YP/WS lakes ($N = 28$) contained large species, but also supported a variety of small fish. C/S lakes ($N = 11$) contained only small species, especially *Phoxinus*.

The combination of pH, Area, and DOC provided the best distinction among fish categories ($P < 0.001$, $R^2 = 0.43$). These variables correctly classified 69, 64, and 56% of fishless, C/S, and YP/WS lakes, respectively. A canonical discriminant function (CDF) analysis produced the following equations, after varimax rotation of the standardized discriminant function coefficients:

$$(1)\quad \text{CDF1} = 0.88\ \text{pH} + 0.003\ \text{DOC} + 0.82\ \text{Area}$$

$$(2)\quad \text{CDF2} = 0.37\ \text{pH} + 0.77\ \text{DOC} - 0.25\ \text{Area}.$$

CDF1, primarily representing pH and Area, accounted for 65% of the among-groups variance whereas CDF2 represented DOC. Scores on canonical axes 1 and 2 differed among fish categories (MANOVA, Wilks lambda = 0.62, $P < 0.0001$). Fishless lakes differed from both C/S and YP/WS lakes ($P < 0.0001$), and the latter two also differed ($P < 0.05$). Scores for fishless and
C/S lakes were significantly different ($P < 0.05$) on both CDF1 and CDF2 (Fig. 1), with fishless lakes generally more acid and lower in DOC (Table 3). Scores for fishless and YP/WS lakes were significantly different ($P < 0.05$) only on CDF1, mainly because fishless lakes were slightly more acid and much smaller than YP/WS lakes. C/S and YP/WS lakes separated widely on CDF2 due to higher DOC levels in C/S lakes.

Data obtained in 1991 showed that midlake depths differed among fish categories (ANOVA, $P < 0.005$), with YP/WS lakes much deeper (mean = 8.4 m) than both C/S (mean = 4.1 m) and fishless lakes (mean = 4.3 m) (Tukey–Kramer, $P < 0.05$).

Macroinvertebrates

Sixty-five taxa were identified in benthic samples from two or more lakes. Nineteen were combined at higher levels to form five, leaving 51 taxa used in the TWINSPAN analysis. Thirty-seven taxa were identified in sweep samples from only 53 of 65 lakes. All 12 lakes without nekton were YP/WS lakes. Twelve taxa were combined into four, leaving 29 used in the analysis.

For benthic samples, the initial separation by TWINSPAN was between an abundant libelluloid dragonfly-dominated assemblage (Group 1, Fig. 2a), composed of *Leucorrhinia glacialis* and *Cordulia shurtleffi* and including corixids and ceratopogonids, and an impoverished fauna dominated by the dragonfly *Gomphus* (Group 2) (Table 4). An important second dichotomy split the libellulid and cordulid assemblage into two groups: 1a, dominated by *L. glacialis*, and 1b, characterized by a diverse assemblage with sphaeriid clams, the gastropod *Helisoma*, and the trichopteran *Limnephilus* (Fig. 2a). A further dichotomy of Group 2 lakes was less informative.

For sweep samples, TWINSPAN distinguished between a large number of lakes ($N = 39$) dominated by nektonic taxa, including corixids, the notonectids *Buenoa* and *Notonecta*, and the dytiscid *Graphoderus* (Group 1, Fig. 2b), and a smaller number of lakes ($N = 14$) in which nekton were scarce or absent and the surface-dwelling gyrinids *Gyrinus* and *Dineutes* were common (Group 2) (Table 5). Nekton-dominated lakes were further separated into those where corixids were abundant and other nektonic taxa were present (Group 1a, Fig. 2b) and a smaller group ($N = 8$) in which *Helisoma* was common and nekton scarce (Group 1b).

TABLE 2. Number and percentage of lakes occupied by various fish species in C/S and YP/WS fish categories.

Species		C/S	YP/WS
Common name	Scientific name	(N = 11)	(N = 28)
Northern redbelly + finescale dace	*Phoxinus* spp.	9 (82)	6 (21)
Brook stickleback	*Culaea inconstans*	6 (55)	5 (18)
Fathead minnow	*Pimephales promelas*	4 (36)	5 (18)
Iowa darter	*Etheostoma exile*	4 (36)	5 (18)
Pearl dace	*Margariscus margarita*	2 (18)	7 (25)
Golden shiner	*Notemigonus crysoleucas*	1 (9)	3 (11)
Common shiner	*Luxilus cornutus*	1 (9)	6 (21)
Creek chub	*Semotilus atromaculatus*	—	1 (4)
Rock bass	*Ambloplites rupestris*	—	4 (14)
Pumpkinseed	*Lepomis gibbosus*	—	2 (7)
Brown bullhead	*Ameiurus nebulosus*	—	2 (7)
Northern pike	*Esox lucius*	—	1 (4)
Yellow perch	*Perca flavescens*	—	20 (71)
White sucker	*Catostomus commersoni*	—	13 (46)

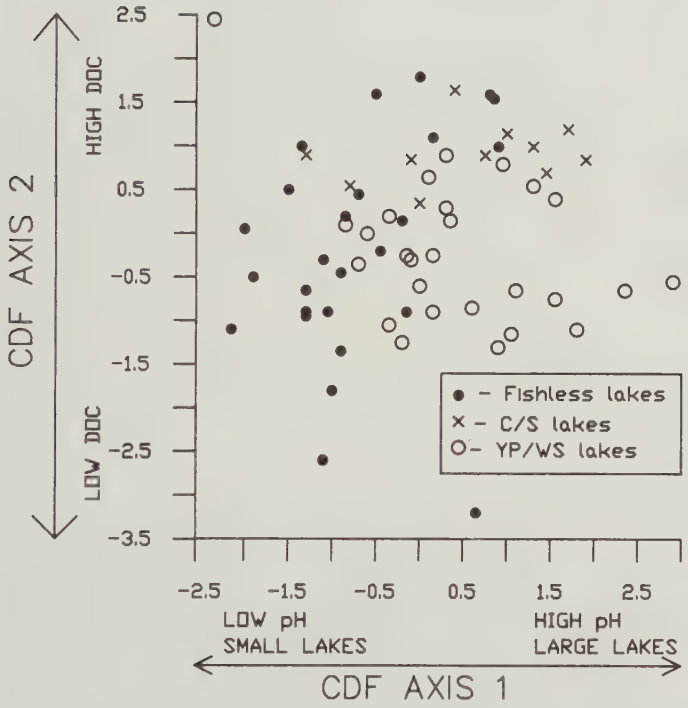

FIG. 1. Canonical discriminant function scores for the 65 lakes, according to fish category.

For benthic TWINSPAN groups, the combination of fish category and pH provided the best discrimination at level 1 ($P < 0.0001$, $R^2 = 0.52$), with the former being more important judging by its loading on the CDF ($|r| = 0.97$). DOC, TP, and Area did not provide significant additional discrimination. Fishless and C/S lakes were associated most often with the Group 1 benthic assemblage whereas YP/WS lakes were usually Group 2 (Table 6). Group 1 and 2 lakes also differed in pH (Table 4); however, its lower loading on the CDF ($|r| = 0.52$) suggests that pH was less important in distinguishing between the numerically abundant and taxonomically rich Group 1 assemblage and the depauperate Group 2 assemblage (Table 4). At level 2, the combination of Alk, TP, and Area discriminated best between benthic Group 1a and 1b lakes ($P < 0.0001$, $R^2 = 0.74$). Alkalinity, which was higher in Group 1b lakes compared with 1a (Table 4), had the highest loading on the CDF ($|r| = 0.83$), indicating that buffering capacity was important in distinguishing between the taxonomically rich Group 1b lakes and the taxonomically poorer Group 1a lakes (Table 4). TP was also important in the discrimination ($|r| = 0.73$), being higher in Group 1b lakes (Table 4).

The first axis of the DECORANA ordination of lakes based on benthic samples accounted for 51% of the variation in macroinvertebrate assemblage characteristics. DECORANA 1 scores differed among fish categories (ANOVA, $P < 0.0001$). Fishless lakes exhibited assemblage characteristics that differed (Tukey–Kramer, $P < 0.05$) from both C/S and YP/WS lakes; the latter two also differed ($P < 0.05$) (Table 3).

The 12 lakes containing no macroinvertebrates in sweep samples were assigned to Group 3 (Table 5). Following a stepwise discriminant function analysis on TWINSPAN Groups 1 and 2 and Group 3, the combination of fish category, Cond, and DOC provided the best discrimination among the three groups ($P < 0.0001$, $R^2 = 0.75$). A CDF analysis produced the following equations:

$$(3)\quad \text{CDF1} = 1.47\ \text{Fish} + 0.10\ \text{Cond} - 0.29\ \text{DOC}$$

$$(4)\quad \text{CDF2} = -0.08\ \text{Fish} + 0.86\ \text{Cond} + 0.53\ \text{DOC}.$$

CDF1, primarily representing fish category, accounted for 69% of the among-groups variance whereas CDF2 represented Cond and DOC. Scores on canonical axes 1 and 2 differed among groups (MANOVA, Wilks lambda = 0.37, $P < 0.0001$). Group 1 lakes differed from both Groups 2 and 3 ($P < 0.01$) whereas the latter two did not differ. Scores for Group 1 lakes were significantly different from Group 2 on both axes (Fig. 3; Table 5), indicating that fish category, Cond, and DOC were important in distinguishing between them (Tables 5 and 6). Group 1 lakes separated from Group 3 primarily on CDF1, suggesting that fish category was the most important variable distinguishing these groups (Table 6).

At level 2 of the TWINSPAN analysis of sweep samples, the combination of fish category, Ca, Area, and TP provided the best discrimination between the two groups ($P < 0.0001$, $R^2 = 0.96$). Fish category was again most highly correlated with the CDF ($|r| = 0.77$). Fishless lakes were associated only with Group 1a whereas C/S and YP/WS lakes were split between the two TWINSPAN groups (Table 6). These results indicate that the absence of fish plays a major role in developing an abundant nektonic fauna, as exemplified by Group 1a. Ca

TABLE 3. Mean,[a] median, and 95% confidence limits (in parentheses) for environmental parameters, canonical discriminant function analysis scores (CDF), and benthic and sweep invertebrate abundance, taxonomic richness, and DECORANA1 scores according to fish category.

		Fishless (N = 26)		C/S (N = 11)		YP/WS (N = 28)	
Parameter	Units	Mean	Median	Mean	Median	Mean	Median
pH		5.3 (5.0–5.7)	5.1	6.5 (6.0–7.1)	6.6	5.9 (5.7–6.2)	5.8
Alk.	$\mu eq \cdot L^{-1}$	2.9 (0.5–8.9)	0.0	68.2 (18.9–240.1)	90.8	10.7 (4.2–25.3)	17.0
Ca	$mg \cdot L^{-1}$	2.7 (2.2–3.4)	2.6	5.3 (3.1–8.9)	3.9	3.6 (3.1–4.2)	3.7
Cond.	$\mu S \cdot cm^{-1}$	39.0 (34.6–44.0)	33.4	44.3 (29.8–65.6)	37.6	35.8 (32.8–39.0)	35.1
TP	$\mu g \cdot L^{-1}$	5.8 (4.9–6.8)	5.9	7.0 (6.1–8.0)	7.1	5.4 (4.2–6.9)	6.0
DOC	$mg \cdot L^{-1}$	5.4 (4.3–6.9)	5.7	8.2 (7.2–9.5)	8.1	5.2[b] (4.5–5.9)	5.0
Area	ha	3.3 (2.5–4.2)	3.1	3.8 (2.0–7.4)	4.4	6.9 (4.3–10.9)	7.5
CDF1	Score	−0.7 (−1.1 to −0.3)	−0.9	0.6 (−0.1–1.3)	0.8	0.4[b] (0.0–0.9)	0.3
CDF2	Score	−0.2 (−0.7–0.3)	−0.3	0.9 (0.7–1.2)	0.9	−0.2[b] (−0.8–0.4)	−0.3
Benthic abundance	$No. \cdot sample^{-1}$	13.1 (9.0–17.1)	10.8	12.2 (4.0–20.4)	9.0	3.9 (2.7–5.2)	2.6
Benthic taxa	$No. \cdot lake^{-1}$	10.8 (9.0–12.7)	10.0	11.3 (8.7–13.9)	10.0	7.8 (6.7–8.8)	8.0
Benthic DECORANA1	Score	81.0 (57.0–105.0)	56.0	174.0 (133.0–215.0)	201.0	255.0 (228.0–282.0)	265.0
Sweep abundance	$No. \cdot sample^{-1}$	11.6 (6.3–16.9)	6.8	3.4 (0.3–6.4)	2.1	1.1 (0.5–1.8)	0.6
Sweep taxa	$No. \cdot lake^{-1}$	5.8 (4.3–7.4)	5.5	7.5 (5.0–10.1)	7.0	1.7 (1.1–2.3)	2.0
Sweep DECORANA1	Score	56.0 (34.0–79.0)	47.0	197.0 (142.0–252.0)	199.0	279.0[c] (223.0–334.0)	314.0

[a]Back-transformed from $\log_e$ values (except pH).
[b]N = 27.
[c]N = 16.

was also highly correlated with the CDF ($|r| = 0.63$) and was higher in Group 1b lakes than Group 1a (Table 5). This difference or that of variables highly correlated with Ca, such as pH ($|r| = 0.89$) or Alk ($|r| = 0.80$), may account for the higher relative frequency of *Helisoma* in Group 1b lakes (Fig. 2b).

The first axis of the DECORANA ordination of the 53 lakes based on sweep samples accounted for 50% of the variation in macroinvertebrate assemblage characteristics. DECORANA 1 scores differed among fish categories (ANOVA, $P < 0.0001$), with each group differing from one another in the order fishless < C/S < YP/WS (Tukey–Kramer, $P < 0.05$). Together with the benthic data, these results suggest that fish predation, or the lack thereof, can impose a gradient effect on macroinvertebrate assemblages with a strong distinction between assemblages in fishless and YP/WS lakes and smaller distinctions between fishless and C/S lakes and between C/S and YP/WS lakes.

Waterfowl

Four species of insectivorous waterfowl were common at Wanapitei: common goldeneye, hooded merganser (*Lophodytes cucullatus*), ring-necked duck (*Aythya collaris*), and black duck (*Anas rubripes*). Broods of goldeneye and black duck were seen proportionately more often on fishless lakes than on either C/S or YP/WS lakes (unplanned G-test, $P < 0.05$) (Table 7). Ring-necked ducks also preferred fishless to YP/WS lakes ($P < 0.05$) but not to C/S lakes. Hooded merganser broods showed no preference ($P > 0.05$), although their use of YP/WS lakes was lower than that of fishless and C/S lakes (Table 7). Overall, watefowl broods preferred fishless lakes over YP/WS lakes ($P < 0.01$) but not over C/S lakes.

Benthic faunas associated with fishless or C/S lakes were preferred over those in YP/WS lakes. All species were found more often on benthic TWINSPAN Group 1 lakes than Group 2 (G-test of independence, $P < 0.01$ for each species) (Table 7). Only goldeneyes exhibited a preference ($P < 0.001$) for Group 1a lakes, selecting acid, fishless lakes over nonacid, fishless or C/S lakes. Use of lakes by ring-neck and black duck broods was related to sweep TWINSPAN groups (Table 7), with Group 1 lakes used more often than Group 2, or lakes in which no invertebrates were found in sweep samples (Group 3) (Fisher exact test, $P < 0.05$). This finding reflects their preference for lakes containing nekton found predominantly in fishless or C/S lakes (Table 3). Both goldeneye and black duck broods preferred Group 1a lakes ($P < 0.05$) and seemed to select fishless lakes which contain an abundant nektonic fauna (Table 5). Use of lakes by mergansers was not related to sweep assemblages defined by any TWINSPAN group (Fisher exact tests, $P > 0.10$).

Discussion

We found strong relationships between the distribution of insectivorous waterfowl broods and the composition of littoral

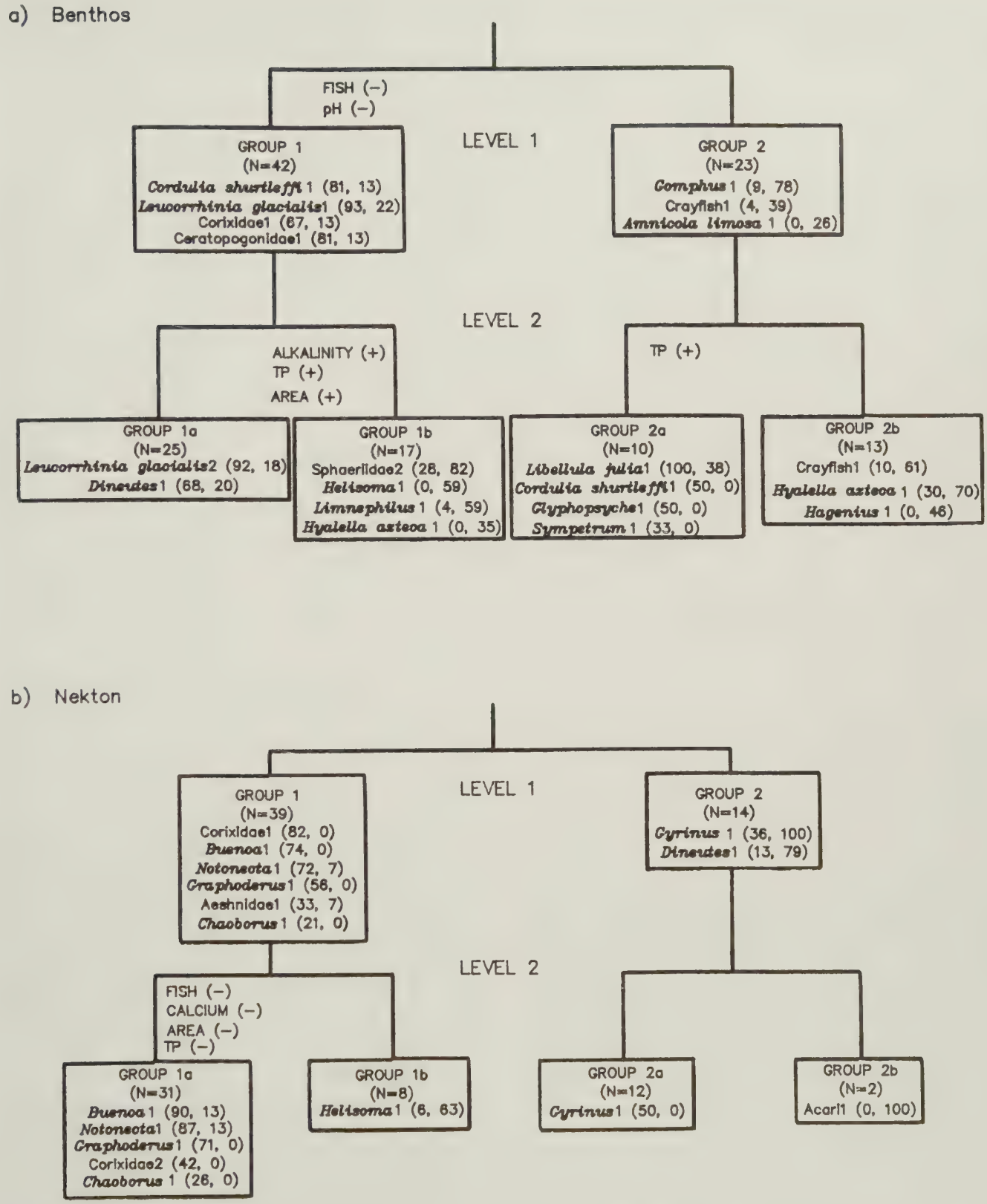

FIG. 2. TWINSPAN classification of lakes to level 2 from (a) benthic sampling (N = 65) and (b) sweep sampling (N = 53). Indicator taxa for each group and explanatory variables are shown. Number affixed to the end of each taxon name represents mean abundance levels: 1 = ($\geq 0.1 \cdot \text{sample}^{-1}$), 2 = ($\geq 1.0 \cdot \text{sample}^{-1}$). Within parentheses, the leftmost number indicates the percentage of lakes belonging to the leftmost group of the TWINSPAN dichotomy in which the taxon was found at the indicated mean abundance level, and the rightmost number indicates the percentage of lakes belonging to the rightmost group of the TWINSPAN dichotomy in which the taxon was found at the indicated abundance level. For explanatory variables, the sign within parentheses represents the direction of effect.

TABLE 4. Mean,[a] median, and 95% confidence limits (in parentheses) for environmental parameters, canonical discriminant function analysis scores (CDF1), and invertebrate abundance and taxonomic richness, based on each pair of dichotomies at the top two levels of the TWINSPAN analysis of benthic samples.

	Benthic TWINSPAN groups									
	First level				Second level					
	1 (N = 42)		2 (N = 23)		1a (N = 25)		1b (N = 17)		2a (N = 10)		2b (N = 13)	
Parameter	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median
pH	5.5 (5.2–5.8)	5.2	6.3 (6.0–6.5)	6.2	5.0 (4.8–5.2)	5.1	6.4 (5.9–6.8)	6.6	6.2 (5.8–6.6)	6.1	6.3 (5.9–6.6)	6.3
Alk. (μeq·L^{-1})	5.0 (1.9–11.7)	0.0	25.4 (10.3–60.8)	29.3	0.7 (0.1–1.7)	0.0	36.5 (8.8–143.0)	80.5	21.7 (4.8–87.1)	21.8	28.7 (7.4–103.6)	85.5
Ca (mg·L^{-1})	3.1 (2.5–3.8)	2.7	4.3 (3.7–5.0)	4.3	2.3 (2.0–2.6)	2.2	4.8 (3.3–7.1)	3.9	4.2 (3.2–5.5)	4.3	4.3 (3.5–5.4)	3.9
Cond. (μS·cm^{-1})	38.5 (34.1–43.4)	33.4	38.2 (34.5–42.4)	37.8	34.3 (32.3–36.5)	32.5	45.6 (34.5–60.3)	40.0	38.3 (32.2–45.6)	38.9	38.2 (33.0–44.2)	36.9
TP (μg·L^{-1})	6.0 (5.4–6.7)	6.0	5.4 (4.0–7.2)	6.0	5.1 (4.4–5.9)	5.3	7.6 (6.8–8.6)	7.2	7.7 (5.8–10.1)	7.8	4.1 (2.5–6.4)	4.4
DOC (mg·L^{-1})	5.8 (4.9–6.8)	6.1	5.6[b] (4.7–6.6)	5.7	5.1 (4.0–6.5)	4.1	7.0 (6.0–8.1)	7.2	6.6 (4.9–8.9)	7.1	4.8[c] (4.0–5.8)	4.8
Area (ha)	3.9 (3.0–5.0)	3.9	6.4 (3.7–11.2)	7.1	3.8 (2.8–5.1)	4.1	4.0 (2.5–6.4)	3.8	3.7 (1.3–10.3)	5.8	9.7 (5.1–18.3)	13.4
CDF1 (score)	−0.7 (−1.1 to −0.4)	−1.2	1.3 (1.1–1.6)	1.4	−1.0 (−1.4 to −0.6)	−1.1	1.5 (0.9–2.1)	1.9	0.6 (0.1–1.1)	0.6	−0.5 (−1.2–0.3)	−0.3
Abundance (no.·sample^{-1})	12.0 (8.8–15.2)	9.3	3.5 (2.2–4.7)	2.1	10.1 (8.5–11.6)	9.3	14.9 (7.1–23.1)	9.0	3.5 (0.7–6.2)	1.8	3.4 (2.1–4.8)	2.6
Taxa (no.·lake^{-1})	10.6 (9.3–11.9)	10.0	7.7 (6.5–8.9)	8.0	8.7 (7.6–9.8)	9.0	13.4 (11.0–15.7)	12.0	6.9 (4.6–9.2)	6.0	8.4 (7.0–9.8)	9.0

[a]Back-transformed from $\log_e$ values (except pH).
[b]N = 22.
[c]N = 12.

macroinvertebrates in small, dilute lakes in the Sudbury area. Broods preferred lakes without large fish species that probably compete for macrobenthic and nektonic prey. In the following sections, we discuss how acidity and fish predation affect littoral macroinvertebrate assemblages and influence the suitability of lakes for waterfowl broods.

Fish

We found that pH helped discriminate between fishless lakes and both C/S and YP/WS lakes. Other studies have shown a relationship between lake pH and fish species' distributions (Wiener et al. 1984; Frenette et al. 1986; Matuszek et al. 1990). Historical losses of fish populations due to acidification have been shown in many Sudbury area lakes (Harvey and Lee 1982; Kelso and Gunn 1984). In Ontario, Matuszek and Beggs (1988) and Minns (1989) demonstrated a decline in fish species richness below pH 6. Lake size also influenced richness (Matuszek and Beggs 1988) and contributed to the discrimination between large YP/WS lakes and small, fishless lakes in this study. High fish diversity may not be possible in these small lakes due to the restricted number and size of distinct habitat types. Size is also related to other features, such as depth, watershed position, and elevation, which affect the likelihood of a lake being colonized by fish. Isolation at higher elevations has been linked to reduced species richness in some Ontario lakes (Minns 1989). The small, nonacid lakes that did not support fish at Wanapitei were isolated from other waterbodies and may never have been colonized by fish. Bendell and McNicol (1987a) showed that lakes with large drainage basins, which are usually large and positioned lower in the watershed, were more likely to support white sucker and a diverse cyprinid assemblage due to access to stream habitat and downstream lakes.

C/S lakes were distinguished from YP/WS lakes by higher levels of DOC, an indicator of their more boglike nature. Species that characterize C/S lakes, *Phoxinus*, brook stickleback, and fathead minnow, often cooccur in stained waters of beaver ponds and small, bog lakes throughout the Precambrian Shield (Scott and Crossman 1973). In contrast, white sucker are usually restricted to larger, deeper lakes (Rahel 1984) whereas yellow perch occupy a broad range of habitats (Tonn and Magnuson 1982; Rahel 1984). The combination of high DOCs and shallow water depths in C/S lakes may result in reduced winter oxygen levels which may be intolerable to large yellow perch (Tonn and Paszkowski 1986) but tolerable to *Phoxinus* and other species (Gee et al. 1978; Klinger et al. 1982).

Macroinvertebrates

The TWINSPAN analyses of benthic and sweep samples identified distinct macroinvertebrate assemblages that were best discriminated by the fish category variable. Group 1 lakes of both benthic and sweep analyses were primarily fishless and C/S lakes whereas benthic Group 2 and sweep Group 3 lakes were predominantly YP/WS lakes (Table 6). At level 2, sweep Group 1a lakes were mostly fishless whereas Group 1b were C/S and YP/WS lakes.

The effects of fish predation on benthic and nektonic assemblages have been well-documented. Eriksson et al. (1980) proposed that the elimination of fish is largely responsible for changes in macroinvertebrate communities in acidifying lakes.

TABLE 5. Mean,[a] median, and 95% confidence limits (in parentheses) for environmental parameters, canonical discriminant function analysis scores (CDF1), and invertebrate abundance and taxonomic richness, based on each pair of dichotomies at the top two levels of the TWINSPAN analysis of sweep samples.

	Sweep TWINSPAN groups											
	First level						Second level					
	1 (N = 39)		2 (N = 14)		3[b] (N = 12)		1a (N = 31)		1b (N = 8)		2a (N = 12)		2b[c] (N = 2)	
Parameter	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median		
pH	5.7 (5.4–6.0)	5.6	5.6 (5.3–5.9)	5.5	6.3 (5.9–6.7)	6.3	5.4 (5.1–5.8)	5.2	6.7 (6.0–7.3)	6.8	5.5 (5.2–5.7)	5.4	6.3	6.8
Alk. ($\mu eq \cdot L^{-1}$)	8.4 (3.3–20.1)	5.2	4.6 (0.8–16.7)	1.3	25.8 (5.7–98.0)	57.5	4.4 (1.4–11.3)	0,0	80.1 (11.0–547.9)	145.3	2.5 (0.1–10.1)	0.0	90.3	96.3
Ca ($mg \cdot L^{-1}$)	3.4 (2.8–4.3)	2.9	2.7 (2.3–3.3)	2.6	4.6 (3.8–5.7)	4.3	2.9 (2.4–3.5)	2.7	6.8 (3.7–12.5)	5.9	2.6 (2.2–3.1)	2.6	2.5	5.3
Cond. ($\mu S \cdot cm^{-1}$)	40.9 (36.1–46.3)	35.4	31.0 (27.9–34.4)	30.8	40.3 (35.0–46.2)	38.7	38.3 (34.4–42.3)	33.6	52.8 (32.8–84.9)	44.6	30.4 (27.2–33.8)	30.8	29.0	42.1
TP ($\mu g \cdot L^{-1}$)	6.3 (5.6–7.1)	6.4	4.7 (2.9–7.4)	6.3	6.6 (5.2–8.4)	5.6	6.3 (5.4–7.2)	6.4	6.2 (5.0–7.8)	6.4	4.3 (3.5–7.0)	5.0	7.7	9.5
DOC ($mg \cdot L^{-1}$)	6.3 (5.4–7.4)	6.0	4.3[d] (3.2–5.9)	4.9	5.4 (4.3–6.9)	5.7	6.3 (5.2–7.6)	6.8	6.5 (4.9–8.7)	7.2	4.0[e] (2.9–5.6)	4.9	4.7	8.9
Area (ha)	3.3 (2.4–4.5)	3.3	7.1 (4.4–11.5)	7.4	8.3 (4.6–15.0)	8.7	2.8 (2.0–4.0)	3.0	6.0 (2.4–14.9)	7.2	8.2 (5.1–13.2)	8.2	1.5	7.0
CDF1 (score)	−0.9 (−1.3 to −0.5)	−1.5	1.2 (0.6–1.5)	1.5	1.6 (1.4–1.8)	1.6	−0.7 (−1.1 to −0.4)	−0.9	2.8 (1.8–3.8)	3.1	ND[f]		ND	
CDF2 (score)	0.3 (−0.1–0.7)	0.2	−0.9 (−1.3 to −0.5)	−1.0	0.0 (−0.4–0.4)	0.0	ND		ND		ND		ND	
Abundance (no.·sample^{-1})	8.8 (5.0–12.6)	4.3	1.9 (1.0–2.9)	1.3	0.0 —	0.0	10.5 (6.0–15.1)	5.3	2.0 (0.9–3.1)	1.8	2.2 (1.0–3.3)	1.5	0.4	0.8
Taxa (no.·lake^{-1})	6.2 (5.0–7.4)	6.0	2.6 (2.1–3.1)	2.5	0.0 —	0.0	6.1 (4.7–7.4)	6.0	6.8 (3.2–10.3)	6.0	2.5 (2.0–3.0)	2.5	2	4

[a]Back-transformed from $\log_e$ values (except pH).
[b]Lakes with no macroinvertebrates in sweep samples.
[c]Actual values presented.
[d]N = 13.
[e]N = 11.
[f]ND = not determined.

The removal of fish from lakes, or their introduction to previously fishless lakes, has resulted in increases or decreases in the abundance of nekton, such as *Chaoborus*, notonectids, corixids, and dytiscids (Macan 1965; Henrikson and Oscarson 1978; Stenson 1978; Oscarson 1987; Evans 1989). Those taxa were more abundant in fishless lakes than in those containing fish in Ontario (Bendell 1986; Bendell and McNicol 1987b). Similarly, Crowder and Cooper (1982) and Mittelbach (1988) found that the mean density, biomass, and individual size of benthos were greater in fishless ponds. Reductions of various taxa, including amphipods, anisopterans, zygopterans, leeches, and pelecypods, due to fish predation have been reported (Post and Cucin 1984; Hambright et al. 1986). Relatively large or mobile anisopterans, such as *Leucorrhinia*, are especially vulnerable to fish predation (Nilsson 1981; Morin 1984; Henrikson 1988).

The impact of fish predation on macroinvertebrates is expected to vary among fish categories due to differences in morphology, especially mouth size, that limit the type and size of prey consumed (Keast and Webb 1966). We observed a gradient from an abundant benthic assemblage in fishless lakes to an impoverished one in YP/WS lakes, with C/S lakes intermediate (Table 3). The small fish of C/S lakes cannot feed on the same large invertebrates eaten by yellow perch and white sucker. Furthermore, an invertebrate's risk of predation is also related to habitat preferences and foraging tactics of fish. *Phoxinus*, which was the most numerous species in C/S lakes, feeds primarily on pelagic zooplankton (Naud and Magnan 1988) and does not seriously affect the larger benthos. In contrast, yellow perch is an effective predator on a wide variety of benthic organisms (Keast and Webb 1966). White sucker is also an effective bottom feeder capable of displacing yellow perch as the main benthivore (Johnson 1977). As for nekton, Bendell and McNicol (1987b) observed that lakes containing only small cyprinids tended to have more nekton than those with perch. We observed greater differences between fishless and C/S lakes in nekton than benthic abundance, indicating that fish species in C/S lakes had a major impact on nekton.

The composition of macrobenthic assemblages was also related to acidity. The benthic Group 1a assemblage consisted of an abundant but relatively species-poor and acid-tolerant fauna (Table 4) found primarily in acid fishless lakes. Group 1b was composed of an equally abundant but species-rich and acid-sensitive fauna found mainly in high-pH fishless and C/S lakes. *Leucorrhinia glacialis*, which was very abundant in Group 1a lakes, is extremely tolerant of acidity and is found in acid bog ponds throughout northern Canada (Walker and Corbet 1975). Sphaeriids, *Helisoma*, and *Hyallela azteca* are acid sensitive (Harvey and McArdle 1986; Økland and Økland 1986; Hunter 1990) and were less abundant in benthic samples from

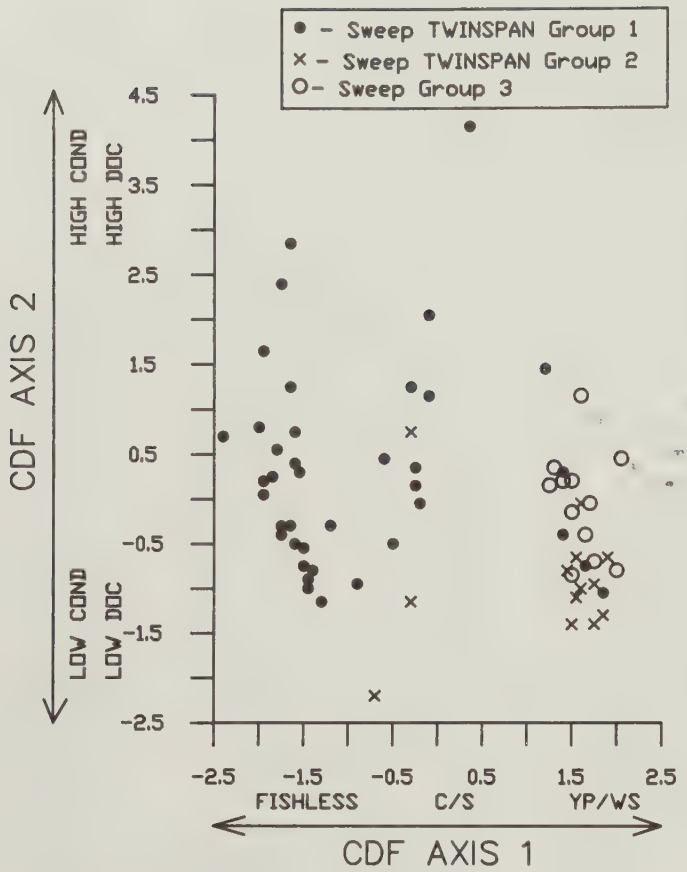

FIG. 3. Canonical discriminant function scores for the 65 lakes, according to sweep-derived macroinvertebrate assemblage type. Groups 1 and 2 are derived from level 1 of the TWINSPAN analysis. Group 3 represents those lakes in which no macroinvertebrates were found in sweep samples.

Group 1a lakes than from Group 1b. *Limnephilus* larvae were also relatively scarce in acid compared with nonacid lakes (Fig. 2a), a finding consistent with the acid sensitivity of *Limnephilus auricula* and *L. lunatus* (Friday 1987) but in contrast with the tolerance exhibited by limnephilids in Norway (Raddum and Fjellheim 1984) and *L. pallens* in Canada (Havas and Hutchinson 1982).

Waterfowl

A rich supply of invertebrate prey is important in habitat selection by waterfowl (Joyner 1980; Murkin and Kadlec 1986; Einarsson 1988; McAuley and Longcore 1988b). At Wanapitei, insectivorous waterfowl preferred lakes containing an abundant macrobenthic and nektonic fauna. Because fish predation plays a major role in determining the composition and abundance of macroinvertebrates in small lakes, we expected to find a strong relationship between the distribution of broods and fish category. Other studies have shown a negative relationship between fish presence and waterfowl habitat selection (Eadie and Keast 1982; Eriksson 1983; McNicol et al. 1987a). However, those studies did not examine patterns of habitat selection among different fish communities. We found an overall order of preference by waterfowl broods for fishless lakes > C/S lakes > YP/WS lakes. The order corresponds to differences in the abundances of benthos and nekton among the three fish categories (Table 3). C/S lakes were less attractive than fishless lakes because they contained less nekton but were more attractive than YP/WS lakes because they had more benthos. Overall, the distribution of waterfowl broods was not related to differences in acidity. The exception was common goldeneye, which preferred lakes containing the species-poor and acid-tolerant benthic fauna of Group 1a lakes over the equally abundant and species-rich but acid-sensitive fauna of Group 1b (Table 7). Goldeneye ducklings eat large numbers of *L. glacialis* (McNicol et al. 1987b), which is extremely abundant in Group 1a lakes.

Avoidance of lakes with large fish predators such as yellow perch and white sucker emphasizes the importance of benthic prey in the diets of insectivorous ducklings. McNicol et al. (1987b) compared gut contents of ducklings taken from both nonacid (pH > 5.5) and acid (pH < 5.5) lakes, including many Wanapitei study lakes, and found that dragonflies (Anisoptera) were the most important item in the diet. On nonacid lakes, most of which contained fish, ducklings relied on immature libellulids but also used other benthic prey, including some acid-sensitive trichopterans and ephemeropterans. At low pH, more odonates, especially *Leucorrhinia*, were consumed. In the

TABLE 6. Number of lakes in each of the indicated benthic and sweep invertebrate groups for each fish category. Groups are based on each pair of dichotomies at the top two levels of the TWINSPAN analysis of benthic samples and sweep samples, respectively.

Sample type	TWINSPAN level	Group	No. of lakes	Fishless (N = 26)	C/S (N = 11)	YP/WS (N = 28)
Benthic	First	1	42	25	10	7
		2	23	1	1	21
	Second	1a	25	19	3	3
		1b	17	6	7	4
		2a	10	1	1	8
		2b	13	0	0	13
Sweep	First	1	39	25	9	5
		2	14	1	2	11
		3[a]	12	0	0	12
	Second	1a	31	25	4	2
		1b	8	0	5	3
		2a	12	1	2	9
		2b	2	0	0	2

[a]Lakes with no macroinvertebrates in sweep samples.

TABLE 7. Percentage of lakes used by waterfowl broods according to fish category, benthic invertebrate groups, and sweep invertebrate groups. Invertebrate groups are based on each pair of dichotomies at the top two levels of the TWINSPAN analysis of benthic samples and sweep samples, respectively.

Faunal type	TWINSPAN level	Group	No. of lakes	Species[a]				
				CG	HM	RNK	BLK	ALL
Fish		Fishless	26	50	38	38	62	81
		C/S	11	9	46	27	18	55
		YP/WS	28	3	14	11	18	39
Benthic	First	1	42	36	40	36	48	79
		2	23	4	9	4	13	22
	Second	1a	25	56	36	36	52	80
		1b	17	6	47	35	42	76
		2a	10	0	20	0	20	30
		2b	13	8	0	8	8	15
Sweep	First	1	39	33	38	36	49	72
		2	14	14	21	7	14	43
		3[b]	12	8	8	8	17	33
	Second	1a	31	42	39	39	58	81
		1b	8	0	38	25	13	38
		2a	12	17	25	7	17	50
		2b	2	ND[c]	ND	ND	ND	ND

[a]Abbreviations: CG = common goldeneye; HM = hooded merganser; RNK = ring-necked duck; BLK = black duck; ALL = all species.
[b]Lakes with no macroinvertebrates in sweep samples.
[c]ND = not determined due to insufficient sample size.

absence of fish, common goldeneye and hooded merganser ducklings increased their use of nektonic organisms compared with those feeding on lakes with fish whereas ring-neck and black ducks ate few nekton (McNicol et al. 1987b). Clearly, for some diving ducks such as goldeneyes which can exploit both benthic and nektonic prey, feeding conditions may improve as lakes acidify and fish disappear (Eriksson 1984). However, conditions may not improve for other diving and most dabbling ducks that are poor nektonic feeders (McAuley and Longcore 1988b). When acid conditions are not severe enough to eliminate large fish competitors, such as yellow perch and white sucker, a shortage of invertebrate prey may result in a stressful situation for waterfowl. Other studies have shown that the growth, feeding behaviour, and survival of ducklings of several species were markedly altered on acidified wetlands compared with control or higher pH sites, even when the effects of fish were considered (DesGranges and Rodrigue 1986; Rattner et al. 1987; McAuley and Longcore 1988a). Reduced survival of ring-neck ducklings in Maine was attributed to increased foraging costs associated with the reduced diversity and quality of prey in low-pH (<6.1) wetlands containing fish (McAuley and Longcore 1988b). Acidity-related reductions in the diversity of prey taken by juvenile waterfowl (McNicol et al. 1987b) and tree swallows (Blancher and McNicol 1991) from acid wetlands have been observed at Wanapitei. Limited dietary calcium in prey from acid sites may have contributed to reduced clutches and decreased growth of swallow nestlings observed near acid wetlands (Blancher and McNicol 1988).

In this study, waterfowl broods did not select lakes containing an abundant, acid-sensitive fauna. However, we did not examine reproductive output in terms of the overall survival of ducklings. Blancher et al. (1992) did investigate the relationship between the presence of breeding waterfowl and lake characteristics from 212 central Ontario lakes, including many from Wanapitei, and found an increased likelihood of observing insectivorous broods as pH increased, independent of fish status. Minns (1981) found that the proportion of lakes that were fishless was much higher in watersheds near Sudbury than elsewhere in Ontario. At Wanapitei, the effects of lake acidification on insectivorous waterfowl are mediated primarily through effects on fish assemblages. In areas where fish assemblages have not been as seriously affected, effects on waterfowl are probably related to direct effects on macroinvertebrates. Implementation of emission controls is expected to curtail or reverse acidification of surface waters in many areas, thus limiting further loss of fish populations. Even under these circumstances, impoverishment of macroinvertebrate faunas in small lakes may continue, possibly leading to increased competition between remnant fish populations and waterfowl for a diminishing prey resource.

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References

BENDELL, B. E. 1986. The effects of fish and pH on the distribution and abundance of backswimmers (Hemiptera: Notonectidae). Can. J. Zool. 64: 2696–2699.

BENDELL, B. E., AND D. K. MCNICOL. 1987a. Cyprinid assemblages, and the physical and chemical characteristics of small northern Ontario lakes. Environ. Biol. Fishes 19: 229–234.

1987b. Fish predation, lake acidity and the composition of aquatic insect assemblages. Hydrobiologia 150: 193–202.

BLANCHER, P. J., AND D. K. MCNICOL. 1988. Breeding biology of tree swallows in relation to wetland acidity. Can. J. Zool. 66: 842–849.

1991. Tree swallow diet in relation to wetland acidity. Can. J. Zool. 69: 2629–2637.

BLANCHER, P. J., D. K. MCNICOL, R. K. ROSS, C. H. R. WEDELES, AND P. MORRISON. 1992. Towards a model of acidification effects on waterfowl in eastern Canada. Environ. Pollut. 78: 57–63.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

DESGRANGES, J.-L., AND M. DARVEAU. 1985. Effect of lake acidity and morphometry on the distribution of aquatic birds in southern Quebec. Holarct. Ecol. 8: 181–190.

DESGRANGES, J.-L., AND J. RODRIGUE. 1986. Influence of acidity and competition with fish on the development of ducklings in Quebec. Water Air Soil Pollut. 30: 743–750.

DILLON, P. J., N. D. YAN, AND H. H. HARVEY. 1984. Acidic deposition: effects on aquatic ecosystems. Crit. Rev. Environ. Control 13: 167–194.

EADIE, J. M., AND A. KEAST. 1982. Do goldeneyes and perch compete for food? Oecologia 55: 225–230.

EINARSSON, A. 1988. Distribution and movements of Barrow's Goldeneye, *Bucephala islandica*, young in relation to food. Ibis 130: 153–163.

ERIKSSON, M. O. G. 1979. Competition between freshwater fish and goldeneyes (*Bucephala clangula*) for common prey. Oecologia 41: 99–107.

1983. The role of fish in the selection of lakes by non-piscivorous ducks: mallard, teal and goldeneye. Wildfowl 34: 27–32.

1984. Acidification of lakes: effects on water birds in Sweden. Ambio 13: 260–262.

ERIKSSON, M. O. G., L. HENRIKSON, B. L. NILSSON, G. NYMAN, H. G. OSCARSON, A. E. STENSON, AND K. LARSSON. 1980. Predator–prey relations important for the biotic changes in acidified lakes. Ambio 9: 248–249.

EVANS, R. A. 1989. Response of limnetic insect populations of two acidic, fishless lakes to liming and brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 46: 342–351.

FORD, J. 1989. The effects of chemical stress on aquatic species composition and community structure, p. 109–144. *In* S. Levin, M. Harwell, J. Kelly, and K. Kimball [ed.] Ecotoxicology: problems and approaches. Springer-Verlag, New York, NY.

FRENETTE, J.-J., Y. RICHARD, AND G. MOREAU. 1986. Fish responses to acidity in Quebec lakes: a review. Water Air Soil Pollut. 30: 461–475.

FRIDAY, L. E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. Freshwater Biol. 18: 87–104.

GEE, J. H., R. F. TALLMAN, AND H. J. SMART. 1978. Reactions of some great plains fishes to progressive hypoxia. Can. J. Zool. 56: 1962–1966.

GUNN, J. M., AND W. KELLER. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (Lond.) 345: 431–433.

HAMBRIGHT, K. D., R. J. TREBATOSKI, R. E. DRENNER, AND D. KETTLE. 1986. Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. Can. J. Fish. Aquat. Sci. 43: 1171–1176.

HARVEY, H. H., AND C. LEE. 1982. Historical fisheries changes related to surface pH changes in Canada, p. 45–55. *In* R. Johnson [ed.] Acid rain/fisheries: Proc. Int. Symp. Acidic Precip. Fisheries Impacts in Northeastern North America. American Fisheries Society, Bethesda, MD.

HARVEY, H. H., AND J. M. MCARDLE. 1986. Composition of the benthos in relation to pH in the La Cloche lakes. Water Air Soil Pollut. 30: 249–262.

HAVAS, M., AND T. C. HUTCHINSON. 1982. Aquatic invertebrates from Smoking Hills, N.W.T.: effect of pH and metals on mortality. Can. J. Fish. Aquat. Sci. 39: 890–903.

HE, X., AND D. M. LODGE. 1990. Using minnow traps to estimate fish population size: the importance of spatial distribution and relative species abundance. Hydrobiologia 190: 9–14.

HENRIKSON, B. I. 1988. The absence of antipredator behaviour in the larvae of *Leucorrhinia dubia* (Odonata) and the consequences for their distribution. Oikos 51: 179–183.

HENRIKSON, L., AND H. G. OSCARSON. 1978. Fish predation limiting abundance and distribution of *Glaenocorisa p. propinqua*. Oikos 31: 102–105.

HILL, M. O. 1979a. TWINSPAN — a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, NY.

1979b. DECORANA — a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, NY.

HUNTER, R. D. 1990. Effects of low pH and low calcium concentration on the pulmonate snail *Planorbella trivolis*: a laboratory study. Can. J. Zool. 68: 1578–1583.

JEFFRIES, D. S. 1984. Atmospheric deposition of pollutants in the Sudbury area, p. 117–154. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons Inc., Toronto, Ont.

JEFFRIES, D. S., W. A. SCHEIDER, AND W. R. SNYDER. 1984. Geochemical interactions of watersheds with precipitation in areas affected by smelter emissions near Sudbury, Ontario, p. 195–241. *In* J. Nriagu [ed.] Environmental impacts of smelters. John Wiley and Sons Inc., Toronto, Ont.

JOHNSON, F. H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34: 1633–1642.

JOYNER, D. E. 1980. Influence of invertebrates on pond selection by ducks in Ontario. J. Wildl. Manage. 44: 700–705.

KEAST, A., AND D. WEBB. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845–1874.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. Water Air Soil Pollut. 29: 765–774.

KELLER, W., J. R. PITBLADO, AND J. CARBONE. 1992. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 25–32.

KELSO, J. R. M., AND J. M. GUNN. 1984. Responses of fish communities to acidic waters in Ontario, p. 105–131. *In* G. Hendrey [ed.] Early biotic responses to advancing lake acidification. Acid precipitation series. Butterworth Publishers, Toronto, Ont.

KELSO, J. R. M., M. A. SHAW, C. K. MINNS, AND K. H. MILLS. 1990. An evaluation of the effects of atmospheric acidic deposition on fish and the fishery resource of Canada. Can. J. Fish. Aquat. Sci. 47: 644–655.

KLINGER, S. A., J. J. MAGNUSON, AND G. W. GALLEPP. 1982. Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*), and brook stickleback (*Culaea inconstans*) for low oxygen in winter. Environ. Biol. Fishes 7: 113–120.

MACAN, T. T. 1965. Predation as a factor in the ecology of water bugs. J. Anim. Ecol. 34: 691–698.

1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Camb. Philos. Soc. 52: 45–70.

MATUSZEK, J. E., AND G. L. BEGGS. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

MATUSZEK, J. E., J. GOODIER, AND D. L. WALES. 1990. The occurrence of cyprinids and other small fish species in relation to pH in Ontario lakes. Trans. Am. Fish. Soc. 119: 116–125.

MCAULEY, D. G., AND J. R. LONGCORE. 1988a. Survival of juvenile ring-necked ducks on wetlands of different pH. J. Wildl. Manage. 52: 169–176.

1988b. Foods of juvenile ring-necked ducks on wetlands of different pH. J. Wildl. Manage. 52: 177–185.

MCNICOL, D. K., B. E. BENDELL, AND R. K. ROSS. 1987a. Studies of the effects of acidification on aquatic wildlife in Canada: waterfowl and trophic relationships in small lakes in northern Ontario. Can. Wildl. Serv. Occas. Pap. 62: 76 p.

MCNICOL, D. K., P. J. BLANCHER, AND B. E. BENDELL. 1987b. Waterfowl as indicators of wetland acidification in Ontario. Int. Counc. Bird Preserv. Tech. Publ. No. 6: 149–166.

MILLS, K. H., AND D. W. SCHINDLER. 1986. Biological indicators of lake acidification. Water Air Soil Pollut. 30: 779–789.

MINNS, C. K. 1981. Acid rain: a preliminary estimate of the risk to Ontario's inland fisheries. Can. MS Rep. Fish. Aquat. Sci. 1622.

1989. Factors affecting fish species richness in Ontario lakes. Trans. Am. Fish. Soc. 118: 533–545.

MINNS, C. K., J. E. MOORE, D. W. SCHINDLER, AND M. L. JONES. 1990. Assessing the potential extent of damage to inland lakes in eastern Canada to acidic deposition. III. Predicted impacts on species richness in seven groups of aquatic biota. Can. J. Fish. Aquat. Sci. 47: 821–830.

MITTELBACH, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69: 614–623.

MORIN, P. J. 1984. Odonate guild composition: experiments with colonization history and fish predation. Ecology 65: 1866–1873.

MUNIZ, I. P. 1991. Freshwater acidification: its effects on species and communities of freshwater microbes, plants and animals. Proc. R. Soc. Edinburgh 97B: 227–254.

MURKIN, H. R., AND J. A. KADLEC. 1986. Relationships between waterfowl and macroinvertebrate densities in a northern prairie marsh. J. Wildl. Manage. 50: 212–217.

NAUD, M., AND P. MAGNAN. 1988. Diel onshore–offshore migrations in northern redbelly dace, *Phoxinus eos* (Cope), in relation to prey distribution in a small oligotrophic lake. Can. J. Zool. 66: 1249–1253.

NILSSON, B.-I. 1981. Susceptibility of some odonata larvae to fish predation. Verh. Int. Ver. Limnol. 21: 1612–1615.

ØKLAND, J., AND K. A. ØKLAND. 1986. The effects of acid deposition on benthic animals in lakes and streams. Experientia 42: 471–484.

OSCARSON, H. G. 1987. Habitat segregation in a water boatman (Corixidae) assemblage — the role of predation. Oikos 49: 133–140.

POST, J. R., AND D. CUCIN. 1984. Changes in the benthic community of a small precambrian lake following the introduction of yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. 41: 1496–1501.

RADDUM, G. G., AND A. FJELLHEIM. 1984. Acidification and early warning organisms in freshwater in western Norway. Verh. Int. Ver. Limnol. 22: 1973–1980.

RAHEL, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology 65: 1276–1289.

RATTNER, B. A., G. M. HARAMIS, D. S. CHU, C. M. BUNCK, AND C. G. SCANES. 1987. Growth and physiological condition of black ducks reared on acidified wetlands. Can. J. Zool. 65: 2953–2958.

SAS INSTITUTE INC. 1988. SAS user's guide: statistics. 1988 ed. SAS Institute Inc., Cary, NC. 1028 p.

SCHEUHAMMER, A. M. 1991. Effects of acidification on the availability of toxic metals and calcium to wild birds and mammals. Environ. Pollut. 71: 329–375.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SCHINDLER, D. W. 1988. Effects of acid rain on freshwater ecosystems. Science (Wash., DC) 239: 149–157.

SCHINDLER, D. W., S. E. M. KASIAN, AND R. H. HESSLEIN. 1989. Biological improverishment in lakes of the midwestern and northeastern United States from acid rain. Environ. Sci. Technol. 23: 573–580.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco, CA. 573 p.

STENSON, J. A. E. 1978. Differential predation by fish on two species of *Chaoborus* (Diptera, Chaoboridae). Oikos 31: 98–101.

THORP, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos 47: 75–82.

TONN, W. M. 1985. Density compensation in *Umbra–Perca* fish assemblages of northern Wisconsin lakes. Ecology 66: 415–429.

TONN, W. M., AND J. J. MAGNUSON. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63: 1149–1166.

TONN, W. M., AND C. A. PASZKOWSKI. 1986. Size-limited predation, winterkill, and the organization of *Umbra–Perca* fish assemblages. Can. J. Fish. Aquat. Sci. 43: 194–202.

WALKER, E. M., AND P. S. CORBET. 1975. The Odonata of Canada and Alaska. Vol. 3. University of Toronto Press, Toronto, Ont.

WIENER, J. G., P. J. RAGO, AND J. M. EILERS. 1984. Species composition of fish communities in northern Wisconsin lakes: relation to pH, p. 133–146. *In* G. Hendrey [ed.] Early biotic responses to advancing lake acidification. Acid precipitation series. Butterworth Publishers, Toronto, Ont.

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